DIFFERENTIAL EXPRESSION OF UPLAND RICE TRAITS AS INFLUENCED BY SOIL-MOISTURE CONDITIONS

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ABSTRACT

The identification of traits that contribute to high crop quality, especially grain yield, is a major step in planning for trait introgression in rice genotypes. Blanket recommendation of certain cultivars for cultivation across ecology gradients fails to take full advantage of genotype-environment compatibility in terms of superior expression of plant traits. A study was thereby conceived to identify traits that confer distinct genotypic performance under each cultivation condition.Twenty upland rice genotypes comprising interspecific NERICA (Oryza sativa x Oryza glaberrima) and two local 'Ofada' selections were cultivated under natural rainfall, in three locations along a toposequence in a derived savannah ecology with intermittent mid-season to terminal drought. The same genotypes were grown in the screenhouse on the toposequence soils with adequate moisture and imposed reproductive stage moisture stress. Genotype, soil and moisture effects produced significant differences in trait expression. Trait heritability estimates were generally low, the highest was 28.3 for leaf dry weight (LDW) on the field and 33.1 for tiller number (TN) in the screenhouse. There were inconsistencies in the traits that best described genotype performance under different growth conditions. Across the growth conditions,TN leaf number (LN), culm dry weight (CDW), panicle number (PN), grain weight per panicle (GWPPN) and grain weigh per plant (GWPP) were identified by factor and discriminant analyses as the foremost traits in describing rice response under adequate moisture and panicle stage moisture stress. Genotype plus genotype-by-environment interaction (GGE) biplots captured between 61.6% and 75.8% of the genotype variation for GWPP and PN respectively, clustered different growing conditions into groups for different traits but identified genotypes (NERICA) 6, 7 and 14 as having across environment adaptation for CDW, GWPPN and PN respectively.

Keywords: ***Drought, GGE biplots, grain yield, soil penetration resistance***.

INTRODUCTION

Moisture stress in rice, occasioned by early, mid-season and terminal stress, as well as a combination of these have been reported as major sources of reduction in grain yield in upland ecologies. Variable but significant reduction in grain yield in different years and for different rice genotypes have been reported (Pantuwan *et al..*, 2002; Kumar *et al..*, 2008) Grain yield loss of up to 87% was also reported (Kumar *et al..*, 2008). Nassir *et al.* (2017) estimated about 54% reduction in grain production under high moisture stress. Improved drought tolerance in rice has the potential to improve grain production particularly in tropical ecologies where rainfall can be erratic and plants encounter moisture stress at the different growth stages. Kumar *et al.* (2008) had demonstrated that direct selection for grain yield under moisture stress would be beneficial, as significant gain in grain yield through direct selection for grain yield under moisture stress was achieved.

The genetic base of rice genotypes is, however, constantly in a flux due to series of repeated hybridization and introgression. Advantageous expressions of traits are, consequently, often concentrated in many genotypes. Selections from crosses involving *O. sativa x O. glaberrima* have further widened trait variation among genotypes thereby enriching the gene pool for trait selection and for further understanding of trait expression (Africa Rice Center (WARDA)/FAO/SAA, 2008) . This promotes the evolution of genotypes with improved trait quality from hybridization exercises. One of the major steps in the development of drought tolerance in rice is the identification of donor genotypes for trait introgression. Most of the beneficial traits are however susceptible to genotype-environment influences, particularly the underlying influence of moisture and soil types (Ouk *et al..*, 2007; Kumar *et al..*, 2008; Nassir and Alawode, 2016; Olagunju *et al..*, 2018).

The use of more than one planting for analysis that cluster genotypes with similar traits should give a better estimate, especially as non-genetic effects can be eliminated. The differences in genotype performance over soil-moisture complex suggest, however, that breeding ecology-specific genotypes cannot rely in a blanket manner on the findings from a particular location. Shrestha *et al.* (2012) reported that the contribution of grain yield components to the final yield in rice changes with the environmental conditions during cultivation, and the influence of these specific conditions on plant traits, at these stages may, indeed, surpass genetic influence on grain yield.

This study was therefore aimed at exploring the use of multivariate analysis to identify the most important traits that define genotypic performance under different cultivation conditions locations along a toposequence, with the attendant soil and moisture differences. It also aims at the identification of traits that best describe genotype performance across locations and isolation of genotypes with the best ability for specific trait expression across the different environments. This is within the overall objective of identifying genotypic trait expression and combination, specific for each location and advantageous for development of genotypes with drought tolerance specific to different soil-moisture condition.

MATERIALS AND METHODS

Description of experimental genotypes and sites: Twenty rice genotypes comprising NERICA 1 - 18 (Africa Rice Center (WARDA)/FAO/SAA, 2008) and two selections from local 'Ofada' variety (FUNABO 1 *and* 2) were established on the field in the early rainy season of 2017. Plantings were done at three locations representing the crest (CR), middle slope (MS) and the valley bottom (VB) of the toposequence of the Teaching and Research Farm of Olabisi Onabanjo University, Ayetoro, Nigeria. The location has a typical bimodal rainfall pattern with peaks in June and October. The site recorded a total rainfall of 642.6mm and a mean daily temperature of 27.8^{0}C over the cultivation months (June - September, 2017). The field location coordinates are 7^0 14' 20''N, 3^0 2' 42''E at altitude 111.86m above sea level (asl) for CR, 7^0 14' 8''N, 3^0 2' 44''E at 96.93m asl for MS and 7^0 13' 52'' 3^0 2' 47'' at 85.04m asl for VB. The soils of the location had earlier been reported to be similar for some soil variables but different for others (Olagunju *et al..*, 2018). Soil moisture after

rainfall at 6cm depth and field soil penetration resistance were obtained (Tables 1 and 2). The CR, MS and VB soils were also used to establish the genotypes in the screenhouse which was sited at the CR location. For each toposequence soils, the genotypes were exposed to two moisture treatments: full (adequate) moisture application; and reproductive stage moisture stress (RMS).

Field experiment: In each location, plants were established from 3-week old seedlings transplanted with the early rains. Each genotype occupied two row plots arranged within each of the three replicates and structured in a randomized complete block design. There were ten hills per row and a spacing of 30cm within and between rows and plots. Weedings were done manually with hoe at two and six weeks after transplanting (WAT). Fertilizer application was done with NPK (20:10:10) at a rate of 60 kgN ha^{-1} two weeks after transplanting and Urea at 40 $kgNha^{-1}$ applied at maximum tillering. Plots were shielded with fish nets to check damage by birds and rodents. Planting date was delayed till midway in the rainfall season (1st July, 2017) such that the reproductive stage coincided with the mid-season drought that often characterizes the study location from mid August to late September.

Screenhouse experiment: Three-week old plants were transplanted into pots previously filled with 5kg of soils from each of the toposequence. One seedling was maintained per pot. There were two treatments for each toposequence soil (TS): (1) regular watering with each plant receiving an average of 40ml of water daily and (2) nine days of no application of water at maximum tillering/panicle initiation. For each group of soil and treatment, pots were organized following the completely randomized design with four replicates. Pots were kept weed free. Each pot received 50g of NPK (20:10:10) and 15g Urea at 2WAT and maximum tillering respectively. Fish nets were used to shield plants against birds and rodents as done as for the field study.

Data collection: For the field study, data were collected on three plants within the row (six plants/plot) for vegetative and reproductive traits following the procedure described by the Standard Evaluation System for Rice (Anonymous, 2013). Plants were carefully excavated from the soil after heavy watering, following which the roots were recovered. Root length was measured while root thickness and dry weights were determined as described by Ekanayake *et al.* (1985). Field soil moisture content for each location was collected at 6cm depth with soil moisture meter (TZS-1K by Top Instrument, China) at five equally spaced points within each replicate around maximum tillering/panicle appearance, within one hour after rainfall and at three-day intervals thereafter. This stopped when a very light shower of rainfall occurred. Soil penetration resistance (SPR) at 5cm and 10 cm depth were taken with Digital Soil Penetrometer (TYD-2 by Top Instrument, China) about one hour after rainfall and after one week of no rainfall for the toposequence locations. Data on grain yield and vegetative parameters were collected on all plants in the screenhouse as for the field experiment. Roots were washed free of the potted soil and data were taken from them as described above.

Data analyses: Data from soil and plant attributes were subjected to statistical analyses using the GENSTAT package, 12th edition (Payne *et al.*., 2009). Combined analysis of variance was carried out

separately for the field and screenhouse study to determine the effects of the soils and genotypes for the field experiment as well as soil, moisture and genotypes for the screenhouse study. For each of the studies, factor and discriminant multivariate analysis were carried out to reveal the main trait(s) that describe genotypic response towards grain production. The genotype main effect plus genotype-by-environment interaction (GGE) biplot method (Yan *et al.*., 2000) was used to further explore the compatibility of genotypes to planting conditions with emphases on traits identified as most important by the factor and discriminant analyses. Genetic and phenotypic coefficient of variation (GCV and PCV) and broad sense heritability estimates (H) were computed based on the procedure described by (Singh, 1992).

RESULTS

The field toposequence mean soil moisture content (SMC) for days after rainfall (DAR) and mean squares from analysis of variance are presented in Table 1.The crest soil had the highest moisture content (23.91%) a few hours after rainfall but declined with days after rainfall, the effect was acute in the mid slope location with 72.8% reduction compared to 59.7% reduction in the valley bottom. The field location differred significantly ($p<0.01$) in soil moisture content mean squares for days after rainfall, toposequence location and their interaction (Table 1).

TABLE 1. FIELD TOPOSEQUENCE MEAN SOIL MOISTURE CONTENT (SMC) FOR DAYS AFTER RAINFALL (DAR) AND MEAN SQUARES FROM ANALYSIS OF VARIANCE (ANOVA)

DAR	**SMC(%)**			**Se(p<0.05)**
	Crest	**Mid slope**	**Valley bottom**	
0	23.908	16.583	21.258	1.189
3	13.017	11.333	16.633	0.599
6	10.583	8.000	13.042	0.662
9	7.283	4.508	8.575	0.731
Percent decline (0 – 9DAR)	69.5	72.8	59.7	
ANOVA Mean Squares				
	DAR	Toposequence Location (TL)	DAR X TL	Adjusted R^2
df	3	2	6	
SMC	307.56**	74.103**	7.062**	0.958

Df = degrees of freedom; **= significant ($p<0.01$)

The means squares of the analysis of variance and means of the soil penetration resistance (SPR) across the toposequence locations for different depths and soil condition are displayed in Table 2. Significant ($p<0.01$) mean squares were observed for the location, soil condition and soil depth. The interactions were also significant except the toposequence location x soil condition (TL x SC) interaction. The mean SPR of the crest and mid-slope were similar for both wet and dry soil conditions but different from that of the valley bottom. The same trend occurred with SPR readings at 10cm depth while all the locations differred from one another at 5cm depth

TABLE 2. SOIL PENETRATION RESISTANCE (SPR) FOR THE TOPOSEQUENCE LOCATION (TL) AT TWO SOIL DEPTHS (SD) DURING WET AND DRY FIELD SOIL CONDITIONS (SC)

Mean squares of SPR (df)						
Toposequence location (TL)	Soil condition (SC)	Soil depth (SD)	TL x SC	TL x SD	SC x SD	TL x SC x SD
7555.72** (2)	835639.75** (1)	140200.32** (1)	185.90 (2)	2857.79* (2)	24362.01** (1)	9338.34** (2)

	Means			
TL	Soil condition		Soil depth	
	Wet	Dry	5cm	10cm
Crest	183.13[a]	486.54[a]	284.042[b]	385.625[a]
Mid-slope	171.83[a]	484.98[a]	271.9[a]	384.917[a]
Valley Bottom	139.73[b]	437.30[b]	208.6[c]	368.433[b]

*,**: significant at p<0.05 and 0.01 respectively; a,b,c indicate mean separation with LSD (p<0.05). Means with similar letters are not significantly different; df = degrees of freedom

Table 3 presents the mean squares and genetic parameters from different growing conditions defined by toposequence soils and moisture differences. The genotypic effects were significant (p<0.01) for the above ground vegetative traits as well as the panicle and grain traits. Only root dry weight was significantly different (p<0.05) among the root traits. Soil differences also exhibited varying levels of significance for all traits, with grain weight per plant as the only exception. Differences in soil moisture content resulted in significant (p<0.01) variation in root thickness, culm dry weight (CDW), leaf dry weight (LDW), panicle number (PN), panicle length (PL) along with grain weight per plant (GWPP). Generally, only four of the traits: CDW, LDW, PL, PN were consistent in having significant variances across the main effects. The interaction effect was inconsistent for the traits. Notably, panicle number was significant across all the interaction effects. The soil x moisture (S x M) interaction effect was significant for all traits with the exception of root thickness (RT), spikelet number per panicle and panicle length. Grain weight per panicle (GWPPN), GWPP and LN were significant for all the interaction effects except the genotype x moisture (G x M) interaction component. The G x S x M interaction effect was highly significant (p<0.01) for GWPPN and GWPP. The highest phenotypic coefficient of variation (PCV) of 61.6% was recorded by root dry weight though with low genotypic genotypic coefficient of variation (GCV) whereas panicle length had the least PCV of 12.1%. The GCV was generally low, the highest being 16.3% (GWPP) and the least by RT (3.3%). Broad sense heritability estimate was equally low and ranges from 2.1 for root dry weight to 33.1 for tiller number (TN).

The mean squares and genetic parameters of traits of the rice genotypes established along a field toposequence are displayed in Table 4. The traits varied significantly (p<0.01) for the genotype and soil (toposequence) effects except TN and PN respectively. For the G x S interaction component of the variances, only the CDW was significant (p<0.05) among the vegetative traits, while all the panicle and grain traits were significant. As recorded in the screenhouse, root dry weight (RDW) had the largest PCV of 93.6% with a lower but moderate GCV of 46.6%. In contrast, panicle length had the least PCV. The GCV estimates were also generally low with the least value recorded by panicle length while the highest was by RDW.

TABLE 3. MEAN SQUARES AND GENETIC PARAMETERS OF TRAITS FROM COMBINED ANALYSIS OF VARIANCE OF RICE GENOTYPES ESTABLISHED ON TOPOSEQUENCE SOILS AND EXPOSED TO MOISTURE DIFFERENCES AT PANICLE STAGE IN THE SCREENHOUSE.

Variation source/Trait	df	Root length, RL (cm)	Root dry weight, RDW (g)	Root thickness, RT	Culm dry weight, CDW (g)	Leaf dry weight, LDW (g)	Leaf number, LN	Tiller number, TN	Panicle primary branches, PB	Spikelet number per panicle, SNP	Panicle length, PL	Panicle number, PN	Grain weight per panicle, GWPPN (g)	Grain weight per plant, GWPP (g)
Genotype (G)	19	52.51	15.27*	.666	166.41**	13.75**	293.52**	37.542**	49.64**	15138.81**	48.99**	20.48**	11.38**	132.18**
Soil (S)	2	896.18**	299.80**	24.44**	627.92**	161.21**	470.64**	11.91*	33.10*	16656.77**	28.11*	10.06*	7.01*	38.70
Moisture (M)	1	0.21	12.708	10.50**	945.85**	16.39**	251.16	4.22	21.68	3005.00	144.10**	186.25**	1.38	1180.55**
G x S	38	34.46	14.37*	.42	37.77	2.81	97.62**	6.72**	8.56	2130.44	8.944	6.78**	2.65*	43.63**
G x M	19	41.54	8.249	.35	32.95	1.88	41.32	3.964	7.43	2032.15	11.80	7.21**	2.10	17.98
S x M	2	208.20*	65.95**	.335	691.77**	6.93*	3402.38**	140.28**	101.48**	1077.89	21.06	40.45**	51.85**	2121.05**
G x S x M	38	56.88	12.16	.39	46.79*	2.76	71.66*	3.567	11.69*	2574.77	8.683	3.35*	3.08**	42.19**
PCV (%)		26.1	61.6	21.4	28.9	37.8	26.3	28.2	22.6	27.9	12.1	37.2	38.0	39.7
GCV (%)		4.5	8.9	3.3	11.8	16.2	11.1	16.2	9.8	13.4	4.9	14.8	16.2	16.3
H		3.0	2.1	2.3	16.8	18.4	18.0	33.1	18.9	23.0	16.2	15.8	18.1	16.6

df = degrees of freedom; *,**: Significant at p<0.05 and 0.01 respectively; GCV =genotypic coefficient of variability, PCV = phenotypic coefficient of variability, H = broad sense heritability.

TABLE 4. MEAN SQUARES AND GENETIC PARAMETERS OF TRAITS FROM COMBINED ANALYSIS OF VARIANCE OF RICE GENOTYPES ESTABLISHED ALONG A FIELD TOPOSEQUENCE DEFINED BY SOIL DIFFERENCES IN THE EARLY RAIN SEASON OF 2017

Variation source/Trait	df	Root length (cm)	Root dry weight (g)	Root thickness	Culm dry weight (g)	Leaf dry weight (g)	Leaf number	Tiller number	Panicle primary branches$^{\beta}$	Spikelet number per panicle$^{\beta}$	Panicle length$^{\beta}$	Panicle number$^{\beta}$	Grain weight per panicle$^{\beta}$	Grain weight per plant (g) $^{\beta}$
Genotype (G)	19	16.87**	2.06**	0.74**	45.74**	2.48**	66.59**	3.02	8.39**	4577.23**	14.37**	1.86**	8.34**	9.50**
Soil (S)	2	81.42**	10.37**	131.49**	497.90**	42.36**	1301.37**	134.54**	124.01**	82647.06**	512.76**	.39	78.72**	137.53**
G x S	38	7.56	0.61	0.35	16.96*	0.60	26.31	2.03	7.23*	5783.79**	14.62**	2.01**	5.52*	6.98*
PCV		19.0	93.6	21.3	50.7	49.1	32.8	40.3	20.8	27.6	12.0	25.7	41.3	36.3
GCV		7.7	46.6	7.2	24.7	26.1	15.2	9.4	4.4	9.8	1.0	5.0	15.0	11.2
H		16.2	24.7	11.3	23.7	28.3	21.6	5.5	4.5	12.6	0.7	3.8	13.1	9.6

$^{\beta}$ Based on only the crest and valley bottom data as the data from middle slope was meaningless due to drought; df = degrees of freedom; *,**: Significant at p<0.05 and 0.01 respectively; GCV =genotypic coefficient of variability, PCV = phenotypic coefficient of variability, H = broad sense heritability.

TABLE 5. COMMUNALITIES FROM FACTOR ANALYSIS OF RICE GENOTYPES ESTABLISHED UNDER SCREENHOUSE AND FIELD CONDITIONS

Trait	Screenhouse						β Field	
	Crest		Middle slope		Valley bottom		Crest	Valley bottom
	NMS	PSMS	NMS	PSMS	NMS	PSMS		
Culm dry weight (g)	0.717	0.775	**0.955**	0.658	0.771	0.792	0.768	**0.924**
Leaf dry weight (g)	0.781	0.646	0.706	0.766	0.861	0.653	0.829	0.892
Leaf number	0.877	**0.864**	**0.902**	0.779	**0.914**	**0.907**	0.768	**0.899**
Tiller number	**0.942**	**0.906**	**0.854**	**0.929**	0.898	0.871	0.769	0.788
Panicle primary branches	0.772	0.765	0.648	0.595	0.706	0.883	**0.921**	0.860
Spikelet number per panicle	**0.929**	0.801	0.700	0.782	0.883	0.761	0.883	0.642
Panicle length	0.879	0.639	0.737	0.774	0.699	0.653	0.831	0.778
Panicle number	0.839	0.729	**0.903**	0.790	0.871	0.772	0.673	0.746
Grain weight per panicle	0.835	**0.901**	**0.923**	0.797	**0.952**	0.817	**0.917**	0.870
Root length (cm)	0.887	0.761	**0.932**	0.785	0.814	0.848	0.757	**0.899**
Root dry weight (g)	**0.947**	0.784	0.786	0.754	0.894	0.799	0.651	0.609
Root thickness	0.547	0.626	0.522	0.641	**0.963**	0.847	0.611	0.741
Grain weight per plant (g)	0.833	**0.909**	0.788	**0.925**	**0.939**	**0.950**	**0.969**	**0.916**
Principal Components* (Eigen cumulative variance, %)	5 (83.0)	4 (77.7)	4 (79.7)	4 (76.7)	5 (85.9)	5 (81.2)	4 (79.6)	4 (81.3)

*Eigen value above 1.0; Bold figures are for traits with relatively large communalities; β Based on only the crest and valley bottom data as the data from middle slope was meaningless due to drought; NMS= no moisture stress, PSMS = panicle stage moisture stress.

The trait communalities from distinctive factor analysis for each planting are shown in Table 5. Factor analysis captured between 76.7% and 85.9% of the total variances within 4 to 5 significant components. Traits were inconsistent in having largest communality across cultivation conditions. However, GWPP had high communality in six out of the eight plantings, under both the screenhouse and field conditions, compared to other traits. Leaf number, TN and GWPP also recorded high communality in at least four of the cultivation conditions

Table 6 presents the Eigen values, variances and important traits associated to first three discriminant axes from the screenhouse and field plantings. The analysis reflected similar inconsistency in important traits that described the performance of the genotypes under stressed and non-tressed conditions in the screenhouse as well as on the field. Generally, TN, LN, CDW, GWPPN and GWPP had larger correlations across planting conditions. Notably, reduction in panicle length had higher function weight in the field than the screenhouse conditions.

TABLE 6. EIGEN VALUES, VARIANCES AND IMPORTANT TRAITS ASSOCIATED TO FIRST THREE DISCRIMINANT AXES FROM SCREENHOUSE- AND FIELD-PLANTED UPLAND RICE [B]

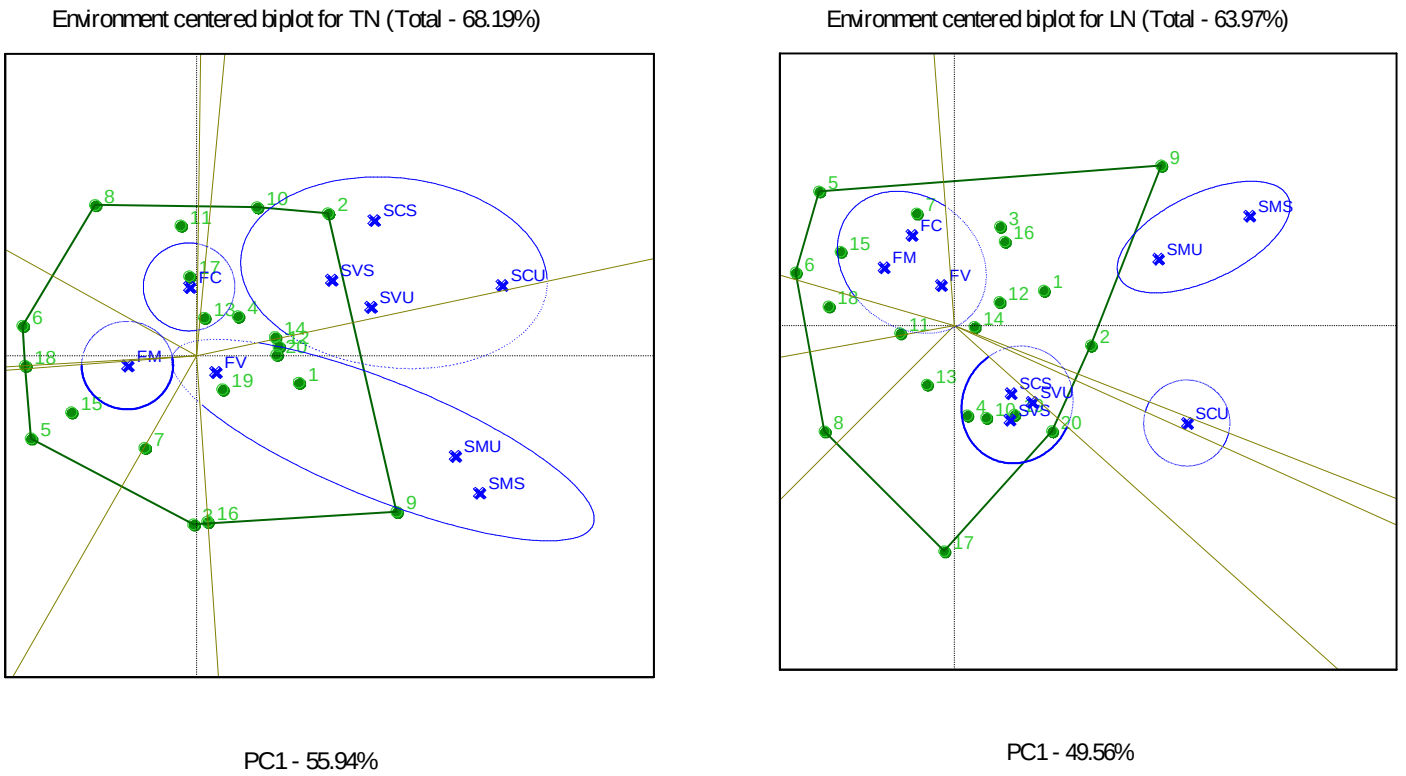
Planting	Canonical function	Eigenvalue	% Variance (cumulative %)	Traits with highest correlation
Crest (SC)				
NMS	1	3.484**	33.3 (33.3)	PN(0.667), CDW(0.355)
	2	2.519*	24.1(57.4)	LDW(0.508)
MTMS	1	5.498**	37.4 (37.4)	CDW(0.518), LDW (0.344), GWPP(-0.323)
	2	2.966**	20.2 (57.5)	SNP (0.385), PL (0.371), GWPP (0.325)
Middle slope (SC)				
NMS	1	5.763**	38.6(38.6)	TN(0.416), PN(0.394), GWPP(0.380
	2	2.973**	19.9(58.5)	GWPP(0.385), GWPPN(0.354)
	3	1.953**	(13.1(71.5)	TN(-0.386), GWPPN(0.378)
MTMS	1	4.894**	45.3(45.3)	TN(0.555), LN(0.413)
	2	1.598*	14.8(60.1)	CDW(0.473), LDW(0.388)
Valley Bottom (SC)				
NMS	1	3.942**	31.4(31.4)	GWPPN(-0.297), LN(0.271), TN(0.264)
	2	2.646**	21.1(52.5)	CDW(0.496), SNP(0.485)
	3	2.127**	17.0(69.5)	PL(0.391), RL(-0.346), GWPPN(0.322)
MTMS	1	2.403**	25.8(25.8)	SNP(0.412), TN(-0.384)
	2	2.091**	22.5(48.3)	TN(-0.458), GWPPN(0.414), LN (0.363)
	3	1.256*	13.5(61.8)	PN(0.561)
Crest (FD)				
	1	9.701**	42.9(42.9)	PL (-0.184), GWPPN (0.169), GWPP (0.165), LN (0.116)
	2	4.082**	18.1(61.0	CDW (0.486), RL (0.433), LN (0.432)
	3	2.513*	11.1(72.1)	PN (-0.333)
Valley bottom (FD)				
	1	16.769**	50.1(50.1)	PL (-0.302), PB (-0.221), CDW (-0.221)
	2	5.258**	15.7(65.8)	SNP (-0.348), LDW (-0.277)
	3	2.787**	8.3(74.2)	SNP (0.699)

*,**: significant at p<0.05 and .01 respectively.TN = Tiller number per plant, LN = leaf number per plant, LDW = leaf dry weight, CDW = culm dry weight, PN = panicle number per plant, PL = panicle length, PB = primary branches per plant, SNP = spikelets number per panicle, GWPPN = Grain weight per panicle, GWPP = grain weight per plant, RL = root length, RDW = root dry weight. SC = Screenhouse, FD = Field, NMS= no moisture stress, PSMS = panicle stage moisture stress.

[β] Field values were computed for only the crest and valley bottom data as the data from middle slope was meaningless due to drought

Figure 1A shows the GGE biplot for number of tillers across the screenhouse and field plantings. Genotype 2 was the best for tillering with the screenhouse crest and valley bottom soils for both stressed and unstressed conditions. Genotype 10 also had good tiller production under the same conditions. Genotype 9 had the best mean tillers in screenhouse middle slope soils for both stressed and unstressed condition as well as valley bottom field planting. Genotypes 8 and 5 were the best for crest and mid slope field plantings though with a concomitant fewer number of tillers.

The GGE biplot for number of leaves across the plantings are displayed in Figure 1B. Genotype 9 had the most number of leaves and this was best expressed in the screenhouse middle slope soils for the two moisture treatments. Genotype 20 had more leaves with screenhouse valley bottom soils and moisture conditions in addition to crest soil with moisture stress. Genotypes produced fewer numbers of leaves in the field locations and were clustered together with genotype 5 being the best.



A **B**

Fig 1. Environment centered GGE biplot for tiller number (TN) per plant (A) and eaf number (LN) per plant (B) of upland rice genotypes (●) under different growth conditions (**X**). Circles represent environment groups. FC = field crest, FM = field middle slope, FV = field valley bottom, SCU = screenhouse crest soil with no moisture stress, SCS = screenhouse crest soil with moisture stress, SMU = screenhouse mid slope soil with no moisture tress, SMS = screenhouse mid slope soil with moisture stress, SVU = screenhouse valley bottom soil with no moisture stress, SVS = screenhouse valley bottom soil with moisture stress.

The growth conditions were separated into two clusters for culm dry weight (Fig. 2A). The field locations were grouped with the screenhouse mid slope soil with adequate moisture (unstressed) and the valley bottom soil with moisture stress. Genotype 6 had the best CDW under these conditions. Genotype 20 had the highest culm dry weight and was best for the other group (SCU, SCS, SMS and SVU).

Figure 2B shows the GGE biplot for genotype and environment markers based on PN. The cultivation conditions were clustered into two groups for panicle number (PN). The first cluster had the markers of all growing conditions except screenhouse SMS, SMU and valley bottom field cultivation (FV). Genotype 14 was the best for PN in the sector. The second group (SMS, SMU, FV) had genotype 9 as the vertex genotype.

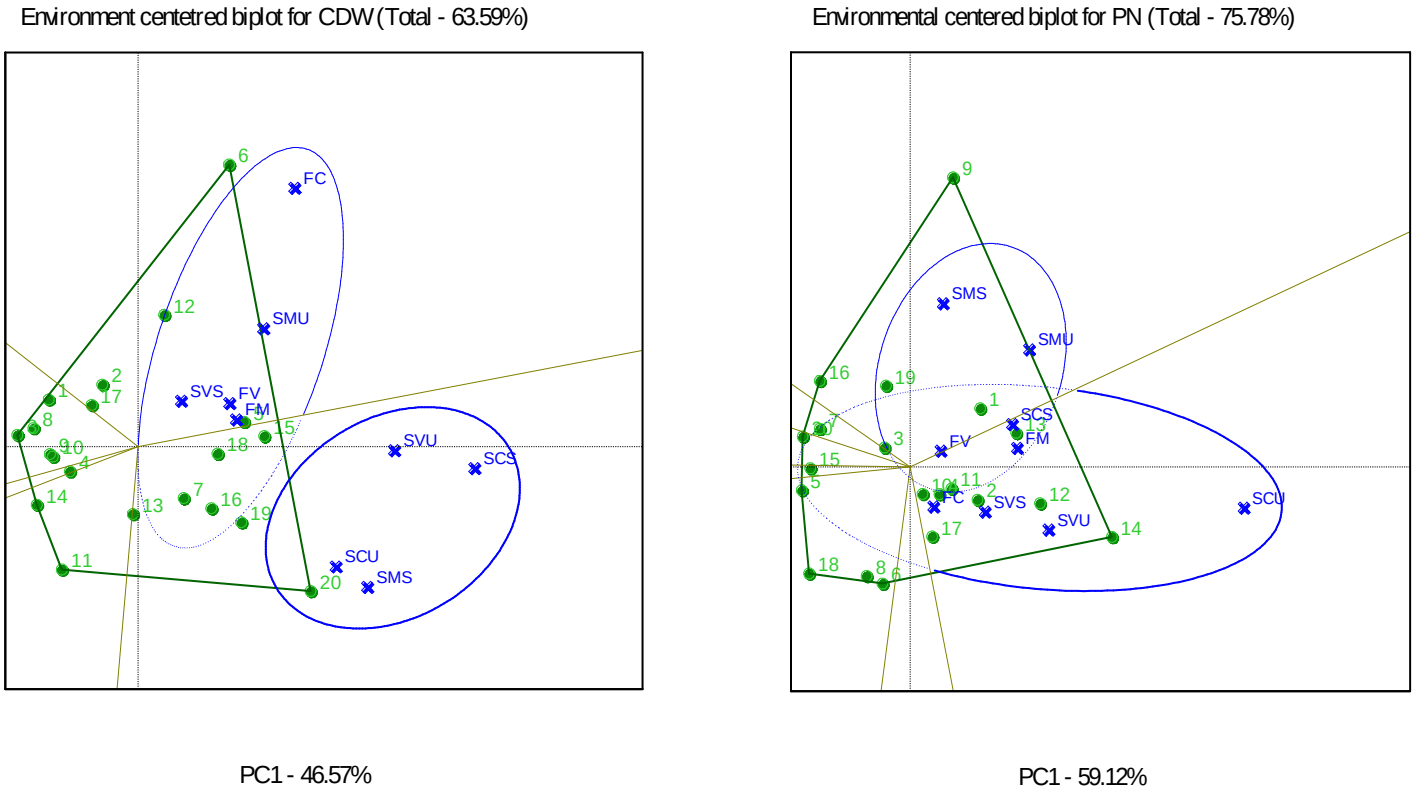


Fig 2. Environment centered GGE biplot for culm dry weight (CDW) per plant (**A**) and panicle number (PN) per plant (**B**) of upland rice genotypes (●) under different growth conditions (**X**). Circles represent environment groups. FC = field crest, FM = field middle slope, FV = field valley bottom, SCU = screenhouse crest soil with no moisture stress, SCS = screenhouse crest soil with moisture stress, SMU = screenhouse mid slope soil with no moisture tress, SMS = screenhouse mid slope soil with moisture stress, SVU = screenhouse valley bottom soil with no moisture stress, SVS = screenhouse valley bottom soil with moisture stress.

The environment centred GGE biplot for grain weight per panicle of upland rice genotypes under different growth conditions is presented in Fig 3A. Genotype 15 was the best for the trait in the sector that featured screenhouse crest soils (stressed and unstressed plants) and middle slope soils without panicle stage moisture stress. The valley bottom field conditions along with screenhouse valley bottom and mid slope soil with moisture stress were highlighted in the sector that had genotype 7 as the best for GWPPN. The genotype was also the overall best for mean and stable GWPPN. Genotype 13 was topmost for grain weight per panicle in the field crest (FC) location.

The genotype and 'environment' markers for the GGE biplot for grain weight per plant are displayed in Fig. 3B. Genotype 2 had the highest mean and was also the most stable for the trait and appeared in the sector that featured screenhouse crest plantings and the middle slope soil with no moisture stress. Genotype 16 had the largest grain weight per plant in the

sector having field crest and valley bottom plantings and also unstressed plants on valley bottom soil. Genotype 13 appeared along with only the stressed screenhouse plants on valley bottom soil.

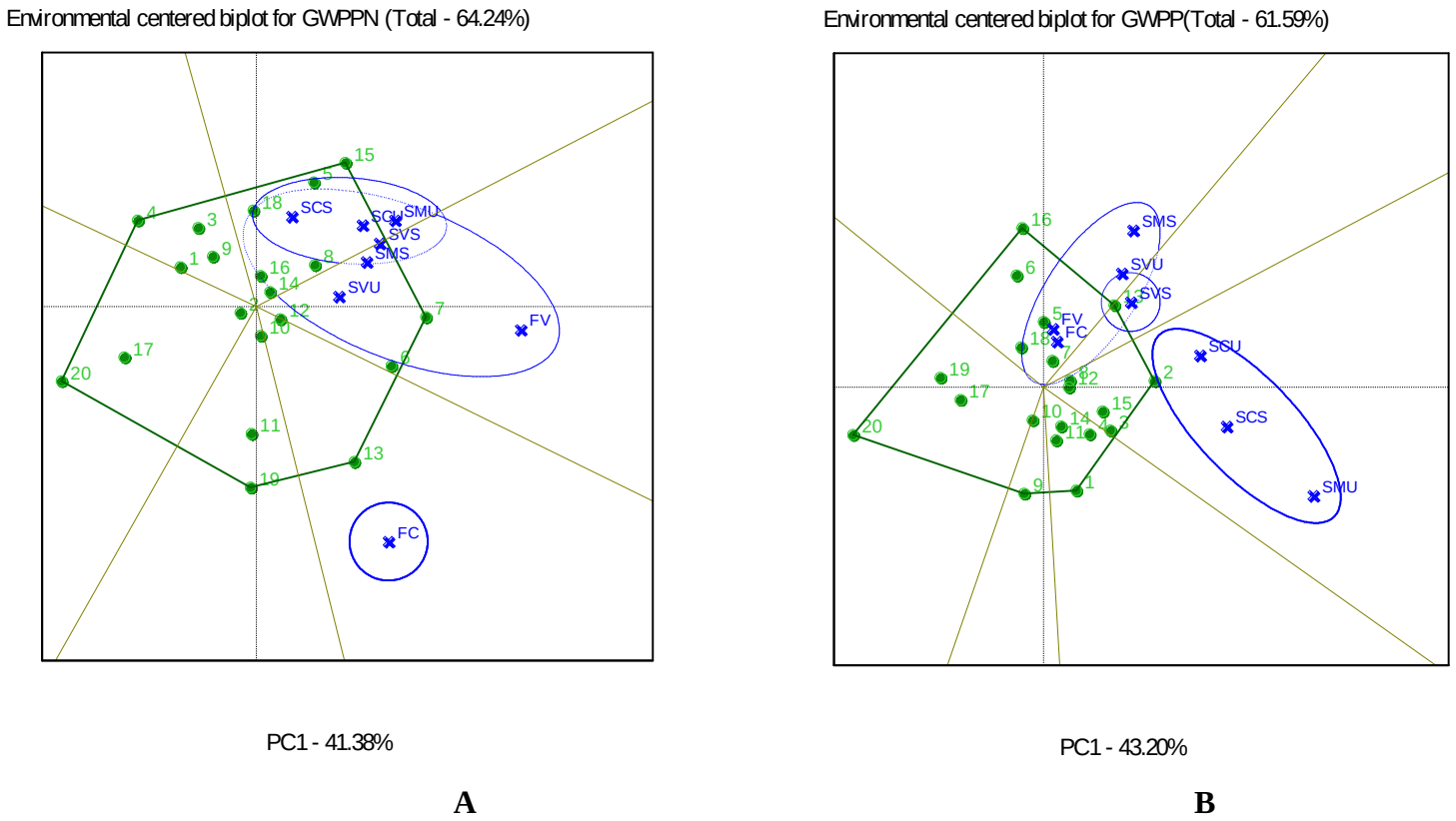


Fig 3. Environment centered GGE biplot for grain weight per panicle (GWPPN) (**A**) and grain weight per plant (GWPP) (**B**) of upland rice genotypes (●) under different growth conditions (**X**). Circles represent environment groups. FC = field crest, FM = field middle slope, FV = field valley bottom, SCU = screenhouse crest soil with no moisture stress, SCS = screenhouse crest soil with moisture stress, SMU = screenhouse mid slope soil with no moisture tress, SMS = screenhouse mid slope soil with moisture stress, SVU = screenhouse valley bottom soil with no moisture stress, SVS = screenhouse valley bottom soil with moisture stress.

DISCUSSION

The significant differences in location moisture content and the decline with number of rainless days, coupled with the significant interaction of these factors is an indication of the contrasting conditions that the genotypes were exposed to during their growth. This is possibly more crucial at the flowering/grain filling stages when moisture limitation can be most felt and genotype response through the yield variables can be complex (Shrestha *et al.*., 2012). Significant mean squares of SPR for location, soil condition and depth as well as their interactions indicate the wide variation in cultivation environment across the toposequence. The differences in moisture

content of the soil across the season would undoubtedly make the growing condition more complex. The response of the rice genotypes would have been influenced by these interactions.

The substantial variations in the vegetative traits may have been a consequence of the field soil variations as well as the genotypic and genotype x soil interaction effects. This alludes to the possibility of further concentration of beneficial genes for increased (or decreased) vegetativeness depending on the breeding goal. The genotypes, particularly the NERICA selections are closely related by virtue of being selected from limited number of parent lines hence the low CV for most traits. (Africa Rice Center (WARDA)/FAO/SAA, 2008). Even at this, further beneficial genetic manipulation for leaf, tiller and culm are still feasible, though the low heritability suggests that this should be from genotype pedigree that would benefit the genotypes in this study. Differences in root weight would be determined by root number, volume and thickness; hence selection for these traits would also be advantageous. This corroborates the findings of Wang *et al.* (2009), Bernier *et al.* (2008), Atlin *et al.* (2008) and Nassir *and* Adewusi (2015) on genotypic differences and contribution of the traits to moisture uptake and drought adaptation. Trait variation as influenced by soil and moisture differences attests to the importance of these factors to full genetic expression for beneficial traits. The complexity of rice environments is further underscored by the significant soil x moisture level effect. Development of rice varieties must take cognizance of these such that blanket recommendation of varieties, even within upland environment may not always pay off.

The field conditions elicited trait expression that was fairly comparable with the screenhouse observations. The soil differences (with the undertone of moisture variation) induced significant trait expression and the possibility of genotype development based on peculiar soil characteristics. The significant soil-genotype interaction for panicle and grain traits points to the inherent instability in grain production and the major influence of soil and its features. The inability of the genotypes to produce meaningful grains in the mid slope location in this study may have derived from the acute loss in soil moisture as the reproductive stage drought persisted.

Inconsistency in trait communalities was to be expected based on the significant differences in trait expression due to the main factors and their interaction. The discriminant analysis also confirmed the inherent instability in traits that best describe genotype performance under variable growing condition. Traits with large communality for most of the growth conditions would give a better representation of genotype performance across cultivation environments. On this premise, selection in favour of higher leaf number, tiller number and grain weight per plant should be advantageous in developing genotypes for cultivation across upland paddy soil and moisture continuum.

In addition, discriminant analysis recognized culm dry weight and grain weight per panicle as also important. Olagunju *et al.* (2018) had highlighted the importance of culm characteristics as strong vegetative feature of rice plant with substantial proportion of assimilate and the eventual notable influence on grain production.

The biplot grouping of growth conditions is not strictly a mega environment representation, but presents opportunity for genotype compatibility to a number of growth conditions. One major advantage of the GGE biplot is its ability to identify environments that elicit similar genotypic response (Gauch, 2006; Yan *et al.*., 2007; Gauch, 2006) The variation in genotype-environment clustering for different traits highlights the intricacies involved in trait response and eventual genotype instability across cultivation conditions. Specifically, however, certain field and screenhouse conditions were grouped together along with some genotypes for a few traits. Such genotypes should be useful in instituting crosses and subsequently selecting genotypes with wider compatibility to differing growth conditions. This case is true for genotype 9 (NERICA 9) for tiller number, genotype 6 (NERICA 6) and 20 (FUNABOR 2) for CDW, genotype 14 (NERICA 14) for panicle number, genotype 7 (NERICA 7) for grain weight per panicle and genotype 16 (NERICA 16) for grain weight per plant. Necessary consideration for best trait expression requires notwithstanding, that genotype 9 (NERICA 9) for leaf number and genotype 2 (NERICA 2) for grain weight per plant receives due attention.

CONCLUSION

Rice response to variable growing conditions through vegetative and grain yield traits is dependent on genotype and soil factors. Results from screenhouse and field plantings were largely similar in confirming the influence of soil and genotype effect on traits. Reproductive stage moisture limitation exhibited differences in trait expression in both. Factor and discriminant analysis identified LN, CDW, TN, PN, GWPPN and GW as the most important traits across genotype-soil-moisture continuum. The significant interaction of the factors was not consistent across most traits for both field and screenhouse plantings. The grouping of environments along with compatible genotypes was not different for different traits. A few genotypes were identified as compatible to variable growing conditions and could serve as the genotype base for a programme of introgression for improved grain production. In this wise, genotype 6(NERICA 6) and genotype 20 (FUNABOR 2) were identified for culm dry weight, genotype 9 (NERICA 9) for panicle and tiller number, genotype 14 (NERICA 14) for panicle number, genotype 7 (NERICA 7) for grain weight per panicle and genotype 2 (NERICA 2) for tiller number and grain weight per plant.

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