

Genetic analysis and genotype x environment interaction for resistance to northern leaf blight disease in tropical maize (*Zea mays* L.) genotypes

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Northern leaf blight (NLB) disease one of the most devastating foliar diseases of maize accounting for more than 50% yield losses annually. Information on inheritance of NLB resistance of maize population adaptable to tropical environments is required. Thus, hybrids generated through 10 x 10 half-diallel of tropical maize inbred lines were evaluated in five environments to determine their combining ability, impact of NLB disease on grain yield, and genotype x environment (G x E). The 45 single cross F₁ hybrids and nine hybrid checks were evaluated across five environments using 9 x 6 alpha lattice with three replications. The greater proportion of general combining ability (GCA) over specific combining ability (SCA) effects across environments implies that additive gene action influences the inheritance of these traits. Predominance of additive gene indicates that rapid progress would be achieved from selection for NLB disease resistance. Regression analysis revealed 1030–1130 kg ha⁻¹ reduction in maize grain yield per increase in NLB severity score. Significant negative relationships ($r = -0.33$ to -0.77) were reported between grain yield and NLB severity scores in this study. This showed the potential of NLB to cause yield reduction in susceptible genotypes. GGE revealed that the test environments fell into two sectors, indicating the existence of two mega-environments and presence of significant crossover interaction.

Key words: maize, northern leaf blight disease, gca, sca, regression

INTRODUCTION

Northern leaf blight (NLB) disease of maize caused by hemibiotrophic ascomycete fungus *Exserohilum turcicum* (Pass.) Leonard and Suggs (syn. *Helminthosporium turcicum* Pass.) is currently one of the most devastating foliar diseases of maize worldwide and now endemic in sub-Saharan Africa (SSA) (Vivek *et al.*, 2010). The disease occurs prevalently under conditions of high humidity and moderate temperature and can be found in most regions where maize is grown (Pratt and Gordon, 2005). The symptoms of the disease are influenced by host-pathogen interactions, pathogen strain, maize genotype, plant age at infection, and climatic conditions. The symptoms generally present small elliptical spots on affected leaves, greyish green in colour and water-soaked lesions with scorched appearance on heavily infected maize field (Levy, 1991). Levy (1991), reported that isolates from different areas were different in parasitic fitness as indicated by infection efficiency, sporulation and lesion size, while isolates of same location showed less variation. Northern leaf blight causes yield loss by damaging photosynthetic tissues of susceptible genotypes. NLB disease of maize results in yield losses of about 50% annually, but losses of up to 100% due to leaf defoliation and

scotching have also been documented depending on maize varieties and time of disease attack (Sibiya *et al.*, 2012). The yield loss portends a great consequence on food security since maize is known to be a predominant staple crop for more than 70% of population in SSA. Numerous reports around the globe revealed that NLB disease is spreading rapidly within the Africa continent with adverse effects on maize productivity (Sibiya *et al.*, 2011). Most maize disease control and management is centered on the use of chemical fungicides and genetic resistance (Gordon *et al.*, 2006), though majority of small-scale farmers in SSA lack the financial resources to make use of fungicide and other control strategies (Ward *et al.*, 1999). Therefore, it would be advisable to breed genotypes with acceptable level of NLB resistance to curb the spread of NLB disease and reduce yield loss of maize. Diverse sources and genetic basis of resistance to NLB have been detected and reported by many researchers (Welz and Geiger, 2000; Sharma and Payak, 1990; Hakiza *et al.*, 2004; Lipps *et al.*, 1997). However, majority of these sources are particular to temperate regions using temperate germplasm that cannot be directly use in tropical regions of Africa. Only a few

sources of resistance have been identified from some tropical and sub-tropical African germplasm (Schechert et al., 1997). CIMMYT (2004) observed high resistance in some of their maize lines viz; CML443, CML444 and CML445, and these lines are adapted to mid-altitude conditions. Therefore, the nature and magnitude of NLB disease resistance need further analysis in some of these maize lines (CIMMYT, 2004). With the grievous implication of this disease on food security, additional sources of NLB disease resistance would be required. This will help to confer resistance to NLB susceptible inbred lines that are high yielding and widely used in hybrid maize production in tropical Africa. The new sources of NLB resistance must be properly characterized, the gene action and combining ability (CA) of the lines should be established. NLB disease resistance has been reported to be controlled by additive gene actions in most of the studies on the quantitative inheritance of NLB (Sigulas et al., 1988; Carson, 1995; Schechert et al., 1997; Vivek et al., 2009). However, Schechert et al. (1997) reported that dominant gene action played a significant role in conferring resistance in some maize genotypes. In SSA, maize production environments are highly variable which results in complicated genotype by environment (G×E) interactions (FAO and CIMMYT, 1997). So, diseases such as NLB are often difficult to manage, since their occurrence over years is difficult to predict due to their high level of dependence on prevailing weather conditions (Vivek et al. 2010). Therefore, most disease severity varies along environments resulting in significant G × E (Levy and Pataky 1992; Egesi et al. 2009). G × E bring about complication in breeding and selection programme for NLB disease resistance as the phenotypic expression of the host may vary across different environments (location and season), because of the sensitivity of pathogen to changes in environment (Carson et al. 2002). A significant G × E for quite number of important foliar diseases of maize have been reported (Vivek et al., 2010). This is because of varying disease pressures as influenced by the prevailing weather conditions in different environments. However, there is still a dearth of information on the mode of NLB disease inheritance for maize germplasm adaptable to tropical environments. This study was therefore carried out to (i) determine the combining abilities, types and magnitude of gene action for NLB disease resistance among selected tropical maize inbred lines, (ii) determine the impact of NLB disease on F₁ hybrid yield derived from a diallel analysis of selected tropical germplasm, and (iii) investigate Genotype × Environment interaction for NLB disease resistance in different environments.

MATERIALS AND METHODS

Screening of inbred lines and generation of diallel crosses

Seventy five (75) maize inbred lines adapted to tropical environments sourced from International Institute of Tropical Agriculture, (IITA) Ibadan, Nigeria. The sourced inbred lines were screened to determine their responses to NLB disease under artificial disease infection under greenhouse condition at the Teaching and Research Farm of the Federal University of Technology, Akure, (T&RF, FUTA). Ten inbred lines selected from the screened genetic materials based on their responses to NLB disease and maturity group (Table 1) were used for generation of the crosses. The selected inbred parents were crossed in a 10 x 10 half diallel mating design at T&RF, FUTA to generate 45 single-cross F₁ hybrids. The 45 F₁ hybrids, parents and controls were evaluated at the Teaching and Research Farm of the Federal University of Technology, Akure, (T&RF, FUTA) Nigeria (7°15'N, 5°15'E, 370m altitude); Teaching and Research Farm, Obafemi Awolowo University, (T&RF, OAU) Ile-Ife, Nigeria (04 ° 33'E, 08 ° 28'N, 244m altitude), and at the isolated experimental field of National Cereal and Research Institute (NCRI, out station). The parents were evaluated in trials adjacent to the hybrid trials

in all the test environments. Planting at T&RF, FUTA were done in May 2016 and April 2017, in T&RF, OAU, planting was done in June 2016 and May 2017 (Ife 2017), while planting was done in August 2016 in NCRI out station, giving a total of five environments.

Table 1. Description of the 10 inbred parents used for the study

Number	Designation	Response to NLB disease infestation	Maturity group
1	TZEEI 82	Susceptible	Extra-early
2	TZEEI 9	Susceptible	Extra-early
3	TZEEI 14	Moderately resistant	Extra-early
4	TZEEI 108	Resistance	Extra-early
5	TZEI 134	Susceptible	Early
6	TZEI 27	Moderately susceptible	Early
7	TZEI 9	Moderately susceptible	Early
8	TZEI 16	Moderately resistant	Early
9	TZEI 14	Resistance	Early
10	TZEI 10	Resistance	Early

Field evaluation of diallel crosses

The 45 single cross hybrids and nine control hybrids varieties were evaluated in cropping seasons across five environments using 9 x 6 alpha lattice design with three replications per environment. Plot sizes for the hybrids and inbred parents in each environment was 5m single row plot, with 75cm inter-row spacing and 25cm intra-row spacing. Two seeds were planted per hill and later thinned to one plant per stand at 21 days after planting (DAP) resulting in population density of approximately 53,333 plants per hectare in each of the test environments. Two border rows of local cultivars were planted on each side of the block. At seven days after planting (7DAP) (2 to 3 leaf stage), 7 days old harvested conidia with a spore concentration of 10⁶ CFU/ml was used to inoculate test plants in each of the test environments using hand held sprayer. Inoculation was done towards evening and each test plant was covered with transparent plastic bag after inoculation to ensure proper spore infectivity. The plastic bags were removed very early the following morning.

Compound fertilizer (NPK 15-15-15) was applied at the rate of 60 kg N, 60 kg P, and 60 kg K ha⁻¹ at 3 weeks after planting immediately after thinning, followed by top dressing with 60 kg N ha⁻¹ 3 weeks later. Gramoxone and atrazine were sprayed for weed control at 5 L ha⁻¹ each of paraquat (1,1' dimethyl-4, 4 bipyridinium) and metolachlor (2-chloro-6'-ethyl-N-(2-methoxy-1-methylethyl)-o-acetoluidide). Herbicides were sprayed at low pressure, using a 20L knapsack sprayer. Manual weeding was done as necessary.

Data collection

NLB disease severity was assessed twice at 5 days before mid-silking (NLB 1) and 12 days after mid-silking (NLB 2), based on visual assessment of the whole plot using a modified rating scale 1–9 rating scale of Soto *et al.* (1982) as follows; 1 = 0%, 2 = <1%, 3 = 1–3%, 4 = 4–6%, 5 = 7–12%, 6 = 13–25%, 7 = 26–50%, 8 = 51–75% and 9 = 75–100% leaf area expressing symptoms of NLB disease. Recorded scores were then grouped into following disease reaction types; 1.0 = symptomless, 2.0–4.0 = resistant, 4.1–5.0 = moderately resistant, 5.1–6.0 = moderately susceptible, 6.1–9.0 = susceptible. Pearson correlation analysis was done using PROC CORR module in the SAS statistical software between NLB1 and NLB 2 scores, and a strong significant positive correlation exist between the two scores ($r = 0.82, \leq 0.001$). However, NLB 2 score was used for the statistical analysis as it showed

the total amount of disease at the end of the season. Data was also recorded for grain yield (kg). For grain yield, ears were harvested on a whole plot basis and the fresh ear weight (kg) determined. Five ears from each plot were shelled to determine moisture content (%) at harvest and shelling percentages. The field weight was then used to estimate the grain yield (t ha⁻¹) adjusted to 12.5% grain moisture content (CIMMYT 1985).

Statistical analysis

NLB disease severity data and grain yield data of the hybrids were subjected to Analysis of variance (ANOVA) using mixed model procedure of the statistical analysis system (SAS) software version 9.2 (SAS Inc 2002). The location-year combinations were considered as environments in the combined ANOVA. The 45 single cross hybrids and nine control were considered as fixed factors, whereas replication, block, and environment were considered random factors. Variations due to hybrids sum of squares was partitioned into general combining ability (GCA) and specific combining ability (SCA) following Griffing's diallel analysis Model I (fixed model), Method IV (F₁'s only), according to the linear model for analysis of variance across environments using DIALLEL-SAS05 program developed by Zhang et al. (2005) adapted to SAS version 9.2 (SAS 2008);

$$Y_{ijkl} = \mu + v_{ij} + r_k + (rv)_{ijk} + e_{ijkl}$$

where Y_{ijkl} is the observed measurement for the ij th cross in the k th replication, and l th environment; μ is the overall mean, v_{ij} is the genotype effect which is equal to $g_i + g_j + s_{ij}$, where g_i and g_j , are GCA effects for the i th and j th parents, respectively; s_{ij} is the SCA effect for the ij th cross; r_k the replication effect; $(rv)_{ijk}$ the interaction between the ij th cross within the k th replication and e_{ijkl} is the error term for the Y_{ijkl} observation. Interaction of G × E was used to test the level of significance of corresponding genetic effects (Zhang and Kang 1997). The environments and replications within environments were considered random and therefore tested against the residual error term. The relative importance of GCA and SCA in predicting progeny performance was determined using the equation:

$$\frac{2K^2_{GCA}}{2K^2_{GCA} + K^2_{SCA}}$$

modified from Baker (1978) by Hung and Holland (2012). In this study, K^2_{GCA} is the variance of effects derived from the mean square of GCA and K^2_{SCA} is the variance of effects derived from the mean square of SCA. Since the total genetic variance among F₁ hybrid is equal twice the GCA component plus the SCA component, the closer this ratio is to unity, the greater the predictability of a specific hybrid's performance based on GCA alone.

Spearman correlation coefficients for the NLB disease severity scores with environments were computed using the META-R v6.0.3 software package. Additionally, simple linear regression analysis was employed to determine the impacts of NLB disease scores on grain yield of the hybrids across environments using MINITAB software version 17.

Genotype × environment analysis

Genotype and Genotype × Environment analysis was done with the aid of PB-Tools version 1.4, using the first two principal components of singular value decomposition (SVD) (Yan 2002). Biplot was also engaged to study the interrelationships amongst environments by constructing lines (environment vectors) from the biplot origin to markers

for the environments. An angle of zero showed +1 correlation, while 90° or -90° angle revealed a correlation of zero, and 180° angle showed -1 correlation (Yan 2002). The vectors length was also used to define the discriminating ability of each of the test environments. A shorter vector shows that the environment was not well represented by PC1 and PC2 (Yan et al., 2007).

RESULTS AND DISCUSSION

Analysis of variance and combining ability estimates of NLB disease score and grain yield

Results of the combined analysis of variance across environments revealed highly significant differences ($P < 0.001$) among the hybrids for both NLB disease severity scores and grain yield (Table 2). The significant mean squares among the hybrids for the measured traits showed that there was adequate genetic variability among inbred lines to permit good progress from selection for improvement of grain yield and NLB resistance adaptive traits. In addition, highly significant mean squares were observed for environment (E), and hybrid × environment interaction across environments for the two traits under consideration. This indicated that the test environments were distinct and that the expression of the traits under consideration would not be consistent in diverse environments. Hybrid partitioning into its components revealed that mean squares for GCA and SCA were highly significant for the two traits studied (Table 2).

Table 2. Analysis of variance for NLB disease scores of 45 F₁ hybrids, tested over five environments

Source	df	NLB (1-9)	yield (t ha ⁻¹)
Env	4	0.60*	4.55**
Hybrid	44	43.63**	86.65**
Rep(Env)	10	0.11**	0.97 ^{ns}
Env*Hybrid	176	1.11**	2.05**
GCA	9	176.93**	279.64**
SCA	35	10.54**	24.60**
GCA*Env	36	0.91**	1.61*
SCA*Env	140	0.87**	0.96 ^{ns}
Error	630	0.41	1.17
GCA(%)		81.10	72.80
SCA(%)		18.90	27.20
GCA:SCA		16.79	11.37

ns = non-significant ($P > 0.05$), *, ** significant at $P \leq 0.05$, $P \leq 0.01$ respectively. GCA: general combining ability, SCA: specific combining ability, Env= environment, Rep = replication

This indicated the importance of both additive and non-additive gene effects for the inheritance of the two traits assessed. This implied that significant breeding progress could be realized when hybridization, back-crossing, and recurrent selection methods are being used for the development of hybrids and synthetic varieties as well as in population improvement. Additionally, these results revealed that the inbreds could be classified into distinct heterotic groups under each research environment, and that superior inbreds with good combining abilities as well as those that can serve as ideal testers can be identified under the contrasting environments. Furthermore, significant effects revealed by SCA mean squares for NLB suggest that non-additive gene effects can also be utilized to develop NLB-resistant hybrid combinations. Interaction of GCA × environment expressed significant differences for both NLB disease severity scores and grain yield, whereas, grain yield had no significant differences for SCA × environment, while NLB disease severity scores expressed significant differences for SCA × environment (Table 2). The

Table 3. Estimate of general combining ability (GCA) effects for NLB disease scores and grain yield for over and across five environments.

Parents	NLB GCA per environment				NLB and Yield GCA across environment		
	Akr 2016	Akr 2017	Ife 2016	Ife 2017	Iba 2016	NLB GCA	Yield GCA
TZEEI 82	1.09**	0.38**	0.77**	1.01**	0.83**	0.95**	-1.67**
TZEEI 9	1.59**	1.04**	1.56**	1.09**	1.54**	1.56**	-1.94**
TZEEI 14	-0.66**	-0.08**	-0.82**	-0.91**	-0.96**	-0.79**	0.91**
TZEEI 108	-1.24**	-1.75**	-1.65**	-1.12**	-1.42**	-1.64**	2.54**
TZEI 134	1.21**	1.46**	0.198**	0.88**	1.29**	1.22**	-0.74**
TZEI 27	0.59**	0.28**	0.23**	0.93**	0.54**	0.73**	-1.79**
TZEI 9	0.88**	0.38**	0.85**	0.38**	1.25**	0.96**	-0.94**
TZEI 16	-0.87**	-0.75**	-0.36**	-0.45**	-0.29**	-0.55**	1.15**
TZEI 14	-0.87**	-0.92**	-0.78**	-0.62**	-0.79**	-0.80**	0.33**
TZEI 10	-1.53**	-1.01**	-1.48**	-1.70**	-2.00**	-1.66**	2.14**

*, ** significant at $P \leq 0.05$, $P \leq 0.01$ respectively

Table 4. Estimates of specific combining ability (SCA) effects for the NLB disease scores in five environments for the set of diallel crosses among ten maize inbred lines.

Parents	TZEEI 82	TZEEI 9	TZEEI 14	TZEEI 108	TZEI 134	TZEI 27	TZEI 9	TZEI 16	TZEI 14	TZEI 10
TZEEI 82										
TZEEI 9	0.39**									
TZEEI 14	-1.46**	0.87**								
TZEEI 108	-0.34*	-0.55**	-0.73**							
TZEI 134	0.01 ^{ns}	-0.01 ^{ns}	-1.66**	0.73**						
TZEI 27	0.03 ^{ns}	-0.32*	-0.50**	-0.92**	0.76**					
TZEI 9	0.79**	-0.48**	0.87**	-0.08 ^{ns}	0.73**	-0.05 ^{ns}				
TZEI 16	0.77**	-0.51**	1.44**	0.89**	-0.37*	0.33*	-1.38**			
TZEI 14	-0.45**	1.01**	0.63**	0.14 ^{ns}	0.48**	0.91**	-0.46**	-1.48**		
TZEI 10	0.27**	-0.40**	0.55**	0.86**	-0.66**	-0.22*	0.08 ^{ns}	-0.03**	-0.78**	

^{ns} non-significant ($P > 0.05$), *, ** significant at $P \leq 0.05$, $P \leq 0.01$ respectively

Table 5. Linear regression and Pearson's correlation analysis of grain yield (t/ha) on the NLB disease scores in five environments

Environment	Regression Parameters			Coefficient of determination (R^2 , %)	Regression equation	Correlation coefficient (r^b)
	Intercept (a)±SE	Slope (b)±SE ^a				
Akure 2016	11.46±0.48	-1.13±0.08		59.08	Yield = 11.46 - 1.13 NLB severity score	-0.77**
Akure 2017	10.67±0.23	-1.04±0.04		56.01	Yield = 10.67 - 1.04 NLB severity score	-0.76**
Ife 2016	10.79±0.34	-1.06±0.05		54.01	Yield = 10.79 - 1.06 NLB severity score	-0.72**
Ife 2017	10.45±0.20	-1.03±0.03		55.93	Yield = 10.45 - 1.03 NLB severity score	-0.30**
Ibadan 2016	10.57±0.27	-1.03±0.04		54.67	Yield = 10.57 - 1.03 NLB severity score	-0.75**

SE = standard error, ** significant at $P \leq 0.001$, ^a is the Linear regression model given as $y = a - bx$

^b is the Pearson correlation coefficients for 45 hybrids

significant interaction of GCA mean squares with environment reported in this study for the measured traits across test environments indicated that parental inbred materials exhibited differential performance in hybrid combination under diverse environmental factors. This results contradicts the views of Kang (1996) that the environments plays significant role in the phenotypic expression of agronomic characters, and overlooking components of environments in the field would reduce progress and advances from selection. Therefore, the significant GCA x Environment interaction suggested the need to select different parental lines for hybrid development under each environment. The significant interaction of SCA

x environment mean squares for the traits under study indicated that the response of the single cross hybrids in terms of these traits varied in the NLB disease infested environments. Probably because environmental factors such as pathogen initial inoculum, soil and climate which might have directly affected the emergence and severity of NLB disease. The significant SCA x environment interaction observed in this study for traits assessed is not unexpected since single cross hybrids are sensitive to environmental factors (Hallauer and Miranda, 1988). GCA effects contributed a greater percentage of the sum of squares than SCA effects (GCA for NLB disease severity (81.10 %) and grain yield (72.80 %), SCA

for NLB disease severity (18.90 %) and for grain yield ($t\ ha^{-1}$) (27.20 %)). The results showed the preponderance of additive gene effects and smaller contribution of dominant action in conferring NLB disease resistance in tropical maize inbred materials used. Therefore, this implies that parent of the crosses can be selected *per se* based on their responses to NLB disease. This would ensure efficient use of resources than estimating the GCA effects first. This result corroborates the observations made in most of the studies on quantitative inheritance of NLB disease using diverse inbred lines that additive gene actions played a major role in NLB resistance (Ohunakin et al., 2020; Sigulas et al., 1988; Carson, 1995; Schechert et al., 1997; Vivek et al., 2009). Relative importance of GCA and SCA effects was tested by expressing it as a ratio of GCA effects to the total genetic effects. The closer the ratio to unity, the greater the predictability based on GCA alone (Baker, 1978). Also, the GCA:SCA ratio expressed the preponderance of additive gene actions against the non-additive gene actions for NLB disease severity and grain yield in this research. The result reported implies that it would be possible to determine the performances of progenies for NLB disease resistance for the materials used based on GCA alone. This result is similar to the results reported by Vivek et al (2010), where additive effects was shown to be more important than non-additive gene effects for Gray Leaf Spot (GLS) disease in subtropical maize germplasm. Also, studies reported by Thompson et al. (1987) and Ulrich et al. (1990) showed 100 % GCA contribution to GLS disease variation in temperate germplasm. Therefore, since the results reported is applicable to specific maize germplasm, the variations reported could be the effects of different maize lines, environments as well as the disease isolates. For disease resistance study, negative GCA and SCA effects are desirable. The GCA effects of the ten parents for NLB disease score and grain yield are presented in Table 3. The GCA effects for parents TZEEI 14, TZEEI 108, TZEI 16, TZEI 14 and TZEI 10 was negative and had highly significant difference across environments. These same parents had positive and highly significant differences for grain yield, indicating that the parents are good general combiners for both NLB disease resistance and grain yield. Positive GCA effects across environments for NLB disease severity scores were revealed by inbred lines TZEEI 82, TZEEI 9, TZEI 134, TZEI 27 and TZEI 9. These inbred lines also expressed negative and highly significant grain yield across environments (Table 3). Estimates of specific combining ability effects (SCA) for the 45 F_1 hybrids are shown in Table 4. Across the test environments, twenty (20) F_1 single hybrids had significant negative SCA effects. Most of the hybrids that expressed significant negative SCA effects for NLB disease score were crosses between parents with varying levels of disease resistance, especially resistant (R) \times susceptible (S) lines, particularly those crossed to susceptible lines TZEEI 82, TZEEI 9, and TZEI 134. Some of these hybrids include; TZEEI 14 (R) \times TZEEI 82 (S), TZEI 14 (R) \times TZEEI 82 (S), TZEEI 108 (R) \times TZEEI 9 (S), TZEI 9 (R) \times TZEEI 9 (S), TZEI 16 (R) \times TZEEI 9 (S), TZEI 16 (R) \times TZEI 134 (MS), TZEEI 134 (MS) \times TZEEI 14 (MR). Therefore, the good performance of the hybrids according to SCA effects corresponded to at least one of the parental inbred lines with a good GCA effect for disease resistance. The results, therefore implies that susceptible parents can be combine with resistant lines to generate resistant hybrids. So, significant SCA effects observed towards reduced pressure is an indication that breeders can take advantage of this non-additive gene action associated with the reduced disease levels by developing single cross hybrids among these inbreds materials. Menkir and Ayodele (2005) reported similar results on the effects of GLS disease on tropical maize adapted to mid-altitude regions, between susceptible and resistant parental lines. Therefore, the significant differences expressed by both GCA and SCA mean squares for the two traits under consideration across environments implied that both the additive and non-additive gene actions participated in the inheritance of NLB disease and grain

yield under the research environments. This shows a possibility for grain yield improvement under NLB disease infestation using either backcrossing, or recurrent selection methods for developing hybrids and synthetics with resistant genes to NLB disease. Also, the results indicate a possibility of selecting a potentially discriminating tester and superior inbred lines with good combining abilities based on their reactions to NLB disease. These results corroborate the results reported in studies of quantitative inheritance of NLB disease using diverse inbred lines (Ohunakin 2021; Vivek et al., 2009; Schechert et al., 1997 and Vieira et al., 2009).

Impact of the NLB disease on maize grain yield

Simple linear regression analysis of the grain yield on the NLB disease severity scores for the five environments revealed significant differences (Table 5). The slope of the regression was negative (-1.03 to -1.13) in all the test environments, revealing that grain yield is being suppressed by 1030–1130 $kg\ ha^{-1}$ per each increase in NLB disease severity score. However, coefficient of determination (R^2) values ranged from 54.01 to 59.08%. This implies that the regression models in all the test environments accounted for less than 59.08% of the total variation through their linear relationship. This showed that NLB disease severity was not the only factors contributing to grain yield in the test environments, which also aligns with the observation that some of the high yielding hybrids all over the test environments are susceptible hybrids. In addition, grain yield had a significant negative correlation (-0.33 to -0.77, $P < 0.001$) with NLB disease severity scores in the test environments (Table 5). This implied that the higher the disease severity, the lower the yield. Again, it also indicates that NLB disease is unpredictable in different seasons and locations because the disease development and severity is highly dependent on conducive weather conditions. The results reported in this study aligned with the results reported on the effects of other maize foliar disease on maize grain yield losses. For instance, Ward *et al* (1999) reported a grain yield reduction of 41.7–43.3 kg/ha for every 1% rise in GLS disease severity. However, in favourable season for GLS disease development, Ward *et al* (1996) reported 38% yield loss for susceptible maize hybrids and 20% loss for moderately resistant hybrids. The ‘Which-won-where’ pattern display in the polygon view assists in estimating possible existence of different mega-environments within the target environment (Yan et al., 2000; Yan and Rajcan, 2002; Yan and Tinker, 2006). Fig. 1 displays a polygon view of the GGE biplot of 45 F_1 hybrids tested across five environments. From the GGE biplots, the first two principal component (PCs) explained 96.20% (PC1 had 88.90% and PC2 explained 7.30%) of the total variation of GGE for NLB disease severity. The biplot showed the most susceptible hybrid(s) per environment and across environments. The biplots’ rays partitioned the plot into six sectors, in which the five environments appear in two sectors. Yan et al., (2007) reported that when different environments fall into different sectors, it reveals that the sectors have diverse high yielding varieties, and also reveals crossover $G \times E$, indicating the possibility of partitioning the environments into mega-environments. This study showed that all the test environments fell into two sectors, implying the existence of two mega-environments and presence of significant crossover interaction. Sector I and sector II have both genotypes and environments (Fig.1). In Fig.1, all the five environments are obvious, environment 1 (E1), environment 2 (E2), environment 3 (E), and environment 4 (E4) fall into sector I (mega environment 1), while environment 5 (E5) fall into sector II (mega environment 2). All the five environments revealed positive PC1 scores and fell in the right-hand side of the biplot (fig. 1 and 2). This shows high NLB disease severity score and good discriminative ability. Therefore, GGE biplot analysis suggested that the environments used to test the responses of different genotypes against the NLB disease could

be partitioned into two mega-environments based on coefficients of infection of NLB reaction.

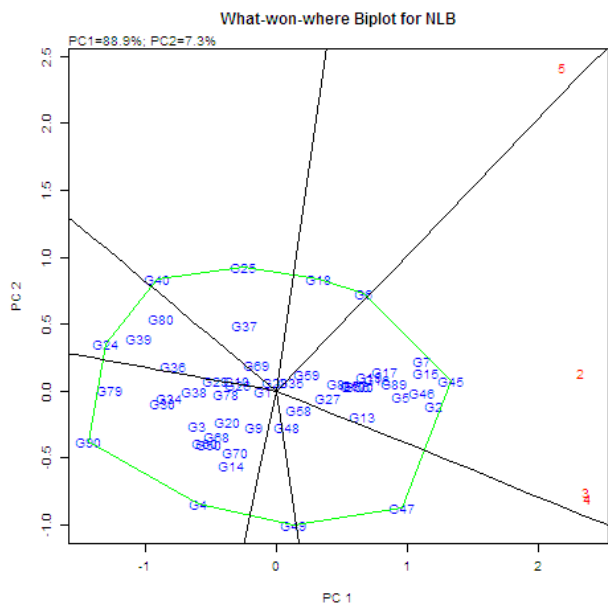


Figure 1. Polygon view of the GGE biplot based on the NLB disease scores (1–9) for five environments. The environments are 1 = Akr 2016 (Akure May 2016 planting), 2= Ife 2016 (Ife June 2016 planting), 3 = Iba 2016 = Ibadan August planting 2016, 4= Akr 2017 (Akure April 2017 planting), 5= Ife 2017 (Ife May 2017 planting).

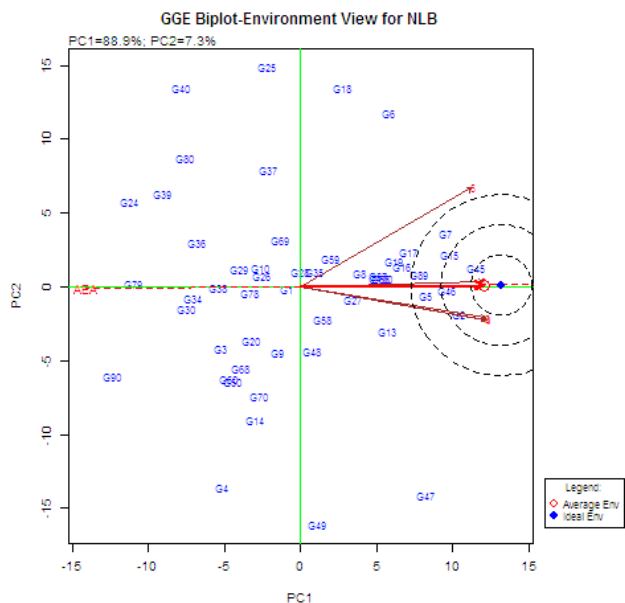


Figure 2. GGE biplot based on NLB disease scores for five environments showing the relationship among the environments. The environments are 1 = Akr 2016 (Akure May 2016 planting), 2= Ife 2016 (Ife June 2016 planting), 3 = Iba 2016 = Ibadan August planting 2016, 4= Akr 2017 (Akure April 2017 planting), 5= Ife 2017 (Ife May 2017 planting).

The cosine of the angle between the vectors of two environments approximates the correlation between them (Yan, 2002). Acute angles show a positive correlation, obtuse angles a negative correlation and right angles no correlation. A short vector may indicate that the test environment is not related to other environments (Yan, 2002). The existing angles between the environment 1(E1) (Akure 2016) and environment 4 (E4) (Akure, 2017) were less than 90°, while the angles that exist between environments 2, 3 and 5 (Ife 2016, Ibadan, 2016 and Ife 2017) were also less than 90°, indicating the existence of high positive correlation among the test environments (Fig.2). The environments which had an acute angle in the GGE biplot suggested a parallel reaction of genotypes (Yan, 2014). Hence, environment 5 (E5) due to its distance from other test environments was ideal test environment for NLB responses based on discriminating ability and representativeness. In fig. 1, G90 (TZEI 14 × TZEI 10), G49 (TZEI 134 × TZEI 14), G47 (TZEI 134 × TZEI 9), G4 (TZEI 82 × TZEI 108), G46 (TZEI 134 × TZEI 27), G8 (TZEI 82 × TZEI 16), G18 (TZEI 9 × TZEI 16), G25 (TZEI 14 × TZEI 134), G40 (TZEI 108 × TZEI 10) and G24 (TZEI 14 × TZEI 108) were the vertex hybrids. The vertex hybrids in the sectors have the highest NLB disease response values or susceptibility for all environments within the sector because of the amount and direction of their distance from the biplot origin. G90 (TZEI 14 × TZEI 10), G24 (TZEI 14 × TZEI 108), G4 (TZEI 82 × TZEI 108), and G40 (TZEI 108 × TZEI 10) were directly opposite and far from the environments which implies that they were the most resistant hybrids in this study. Hybrids located close to the origin would have the same ranking in all environments and was not responsive to the environments.

CONCLUSION

The most resistance inbred lines TZEI 14, TZEI 108, TZEI 16, TZEI 14 and TZEI 10 showed good GCA and contributed negative SCA effects in their respective crosses for NLB disease resistance. The larger percentage of GCA effects of inbreds for both traits under consideration than the proportion of SCA effects across test environments indicated that additive gene action played a predominant role in the inheritance of the measured traits in the single crosses evaluated and that GCA was the main component accounting for the differences among the single-cross hybrids. Preponderance of additive effects indicates that NLB disease resistance could be improved by selection in some of the populations. Also, the study showed that using one parent with resistance would give sufficient NLB disease resistance in single cross hybrids. Also, the results revealed the potential of NLB disease in suppressing grain yield under high disease pressure, indicating the need for resistant genotypes to be planted in NLB disease hot spot regions. Although G × E was observed for the GLS disease, the five environments fell into two mega-environments and presence of significant crossover effects, suggesting variability between the environments in respects to discriminative ability of NLB disease.

AUTHOR CONTRIBUTIONS

The author conceived the research, Setup the research, Collect data, analysed the data, prepare the draft, and make all the corrections

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COMPETING INTERESTS

The author declare that they have no competing interest

ETHICS APPROVAL

Not applicable

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