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Insights into the genetic mechanism for *Turcicum* leaf blight resistance of maize (*Zea mays* L.)

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Abstract

An experiment was conducted to study the genetic mechanism of Turcicum leaf blight (TLB) in maize. A set of 56 experimental F₁ hybrids was screened for TLB under artificial inoculation condition along with standard susceptible and resistant checks. The results revealed that, the inheritance of TLB resistance is majorly governed by additive gene action, while the preponderance of non-additive gene action was displayed by grain yield. The TLB resistance had high narrow sense of heritability. The genetic analysis of parents and hybrids showed sufficient variation for TLB resistance among the studied material. The lines CTLB-01 and CTLB-02 exhibited a high general combining ability effect in a negative direction for Area Under Disease Progressive Curve and percent disease index, which were identified as novel source of durable resistance for TLB. The GGE biplot analysis showed that CTLB-01 and CTLB-02 were genetically similar for disease resistance and IMIC-68 was identified as ideal tester for disease resistance. The CTLB-02 × IMIC-02 and CTLB-02 × IMIC-40 are best crosses for TLB resistance and grain yield. The present findings suggested that the resistance to TLB can be improved through recurrent selection.

Introduction

Maize (Zea mays L.) which has its origin from wild species teosinte (Zea mays subsp. parviglumis) is the third most widely grown cereal crop in the world and in India, after rice and wheat (Murdia et al. 2016). As per the projections made by Erenstein et al. (2021), maize may overtake wheat as the most widely grown crop in the world by 2030 with a 5% increase in area. The demand for maize crops is rising continuously because of its increasing demand from poultry, animal feed, and as industrial raw materials. Accordingly, the production has to be enhanced across the globe and India and has to double its maize production by 2050 to meet this demand (Mehta et al. 2021). Apart from that, ease of cultivation, availability of hybrid seeds, low input cost, and adaptability to mechanization from sowing to harvesting and a constant market price has made it most sought-after crop among farmers and hence cultivated throughout the year (Choudhary et al. 2021).

As corn is cultivated intensively across the seasons throughout the year, its continuous interaction with the environment and has been severely affected by a number of biotic and abiotic stress factors. These stress factors reduce the *per se* value of the crop. Among the different kinds of biotic factors, disease-causing fungal pathogens are of great importance as they cause more economic losses to maize crop across the globe (Yadav et al. 2015). Among the foliar fungal pathogens, *Turcicum* Leaf Blight (TLB) caused by *Exserohilum turcicum* (Pass.) is an important foliar fungal disease of humid regions in maize. This disease is serious in many parts of the world, including India (Carlos 1997).

In India TLB is predominant in Northern hilly regions and in Karnataka during *kharif* season, whereas, in Indo-Gangetic plains, especially in Bihar during the *rabi* season (Lal 1991) causing a yield loss of 2.87 to 51.93 % (Harlapur et al. 2008). Prophylactic management practices have been developed to manage the disease. However, farmers are ignorant and

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are unable to identify the symptoms at the initial stage and take up sprays. Apart from that, during *kharif* season the initiation of the disease also coincides with rains, which adds to the farmers misery and flaring up of the disease. Qualitative or race-specific and quantitative genes control the resistance to turcicum leaf blight (Welz and Geiger 2000). Due to its dynamic nature, E. turcicum continuously develops new virulent strains against qualitative genes. However, quantitative genes show stable performance by increasing both the incubation and latent period (Ullstrup 1970; Carson and Van Dyke 1994). The efficiency of quantitative resistance against the disease has led breeders to use it for developing resistant cultivars. Generally, maize crop improvement programme is mainly directed towards developing heterotic hybrids to enhance productivity per unit area. However, other way of addressing productivity enhancement is through minimizing yield losses due to various stress factors and one among them is breeding for TLB resistance. It is, therefore, necessary to identify resistant sources and utilize them to incorporate the resistance into elite lines to produce high-yielding hybrids combined with disease resistance. Keeping in view the above, the present study was conducted to evaluate the newly developed hybrids against TLB of maize

Materials and methods

Development of material and field evaluation

The material for the present study consisted of 56 F₁hybrids involving seven parental inbred lines, namely, IMIC 69, IMIC 68, IMIC 02, IMIC 40, CTLB 01, CTLB 02 and CML 451 from CIMMYT and CI 4 from IIMR. The crossing was done in 8 × 8 full diallel method to produce the hybrids during *rabi* 2019-2020. These 56 hybrids along with standard checks, were screened for TLB under artificial inoculation condition during *kharif* 2020 along with susceptible, hybrid P-3501 and resistant check GH-150125.

These hybrids along with parental lines were analyzed in two experiments, where both experiments used a randomized complete block design (RCBD) with three replications during *kharif*, 2020 at All India Co-ordinated Maize Improvement Project, MARS, Dharwad. Each entry was raised in two rows of four-meter length with a spacing of 60×20 cm and following all recommended packages of practices. The first experiment was conducted for evaluation of grain yield under normal conditions, while the second experiment was screening of TLB disease incidence under the sick plot done for artificially inoculated conditions.

Isolation and inoculation of pathogen

The fungus, *Exserohilum turcicum* (Pass.) Leonard and Suggs., was isolated by following standard tissue isolation technique from TLB-infected leaves. Sterilized sorghum grains were used for mass multiplication of *E. turcicum* (Joshi

et al. 1969). An artificial epiphytotic field was created using fully colonized sorghum grain cultures following the whorl method of inoculation. The inoculation of mass multiplied culture was done twice at one-week interval from 30 days after sowing and light irrigation was given to create the humid conditions to facilitate the growth of the pathogen.

Observations recorded

To calculate the grain yield, weight of the de-husked ears/ plot was recorded during harvest which is later converted to grain yield at 15 % moisture and expressed in quintals per hectare (q/ha). The intensity of *turcicum* leaf blight was recorded by scoring five randomly selected plants in each treatment at 15 days interval from 45 days after sowing, up to 90 days after sowing as per 1-9 scale (Fig. 1) according to the procedure adopted by Hooda et al. (2018). Severity scores were converted to percent disease index (PDI) as described by Wheeler (1969) and PDI data were transformed using arcsine for analysis. The data is presented, however, in their original percentages.

 $PDI (\%) = \frac{Sum of all numerical grading}{Total number of plants observed \times Maximum disease grade} \times 100$

The PDI values was further utilized to calculate Area Under Disease Progressive Curve (AUDPC) as suggested by Madden et al. (2007) using formula below,

$$A_{k} = \sum_{i=1}^{N_{i}-1} \frac{(y_{i}+y_{i+1})}{2} (t_{i+1}-t_{i})$$

 N_i = Number of consecutive observations; y_i = Disease severity at ith period; y_{i+1} = Disease severity progressing to ith period; $t_{i+1} - t_i$ = time intervals between two consecutive observations

Statistical analysis

The statistical analysis of the data was carried out using RStudio computer software version 1.3.1056. According to Panse and Sukhatme (1962), variance analysis was conducted using mean values. Differences in mean were tested for significance using Duncan test (Duncan 1955). To analyse combining ability, parents and hybrids sum of squares were portioned into general combining ability (GCA) variance, specific combining ability (SCA) variance and reciprocal variance following Griffing's Method 1 Model I of diallel analysis; the Diallel AnalysisR package (Yaseen 2018) in RStudio programme was employed to accomplish this. The model followed is given here under:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + 1/c \sum_{keij}$$

Where, Y_{ij} was the observed measurement of parent indj; μ was the population mean; g_i and g_j were the GCA effects; s_{ij} the SCA effects; r_{ij} reciprocal effects and e_{ij} the random environmental effects associated with i_{jk} th individual. The restrictions imposed on the combining ability effects were:



Fig. 1. A=Disease rating scale; B=Resistant check GH-150125(left) and Susceptible check p3501 (right); C=CTLB-02 × IMIC-02; D=CTLB-01 × CI-4; E=CTLB-02 × CTLB-01; F=CTLB-02 × IMIC-40;G=CTLB-01 × CTLB-02;H=CTLB-01 × IMIC-40;I=CML-451 × IMIC-02; J=CML-451 × CI-4; K=IMIC-40 × CTLB-02

 $\sum g_i = 0$ and $\sum s_{ij} = 0$ for each j (Griffing 1956). The significance of GCA and SCA sources of variation was determined using the error term. The relative importance of GCA and SCA was estimated as the following ratio: $2\sigma^2_{GCA}/[2\sigma^2_{GCA} + \sigma^2_{SCA}]$ where σ^2_{GCA} and σ^2_{SCA} were taken to be the variance components for GCA and SCA, respectively (Baker 1978).

Visualization of diallel data through GGE biplot

The PDI data was used for the purpose of GGE biplot analysis. The PDI values were reversed proportionately, such that higher PDI value denoted higher resistance, i.e., positive and negative PC1 scores denoted resistant and susceptible genotypes. The converted data mean value of parents and crosses were used to form a full diallel matrix, from which the first two principal components are extracted. The statistical method of visualizing diallel data in GGE biplot as described by Yan and Hunt (2002) and Yan and Kang (2003) was used in this study. All biplots presented in this paper were generated using 'GGE Biplots' package (Dumble 2017) of R programme.

Results and discussion

The mean performance of the eight parental lines and 56 hybrids for PDI, AUDPC and grain yield (q/ha) under normal and sick plot conditions and their disease ratings are given in Tables 1 and 2, respectively. Among the inbred lines, CTLB-01 and CTLB-02 recorded the lowest PDI and low AUDPC values for TLB under sick plot (Table 1) compared with others. Hence, were found to be resistant to TLB. The highest PDI was observed in inbred check CM-111 (77.78) followed by CM-202 (73.61) followed by another selected parental inbred line IMIC-69 (68.06), therefore these were found to be susceptible for TLB disease. For grain yield under sick plot (artificial inoculation) conditions, CTLB-01 recorded highest grain yield of 37.74 g/ha followed by IMIC-68 (33.48 q/ha) and CTLB-02 (35.87 q/ha) while the susceptible inbred check CM-202 recorded lowest grain yield of 8.17 g/ha. Although IMIC-68 recorded the highest grain yield, CTLB-02 recorded higher PDI (51.39) than CTLB-02 and was grouped as a moderately resistant line. Thus, may be considered as a slow blighter. Hence the disease might have developed in later stages, whereas yield was not much affected.

Similarly, the grain yield of these parental lines under normal situations was not affected to a great extent. The inbred line CI-4 recorded the highest grain yield (43.04 q/ ha) (highly productive) followed by CTLB-01 (41.47 q/ha) and CTLB-02 (36.70 q/ha), whereas CM-202 the susceptible check recorded only 13.15 q/ha. However, considering both resistances to TLB and grain yield CTLB-01 was the most promising inbred line followed by CTLB-02.

Among the hybrids, CTLB-01 × IMIC-02 recorded the lowest PDI and AUDPC values of 29.17 and 1383.33, respectively (Table 2) under sick plot indicating TLB resistance. Since the grain yield is also equally important, the cross between CTLB-02 and IMIC-02 was found to be the most promising hybrid combination as it not only recorded resistant reaction but also recorded higher grain yield under both sick plot (77.27 q/ha) and optimal situation (88.90 q/ ha) followed by cross combination, CTLB-02 × IMIC-40. The hybrid, IMIC-68 × CTLB-02, had recorded the lowest PDI of 29.17 for TLB but for grain yield it was found poor with 30.49 q/ha under sick plot conditions indicating that combination was not superior regarding yield. As compared to the test hybrids, the resistant check hybrid, GH-150125 recorded highest grain yield of 72.79 and 74.88 g/ha under sick plot and normal situation, respectively with low PDI (32.22) and AUDPC (1533.33). Contrastingly, the susceptible check P-3501 recorded overall the highest PDI of 81.70 among all the hybrids under evaluation and so also highest AUDPC values of 3866.67 and lower grain yield of 32.45 g/ha under sick plot condition as expected, indicating that there was sufficient disease pressure in the experimental plot.

The ANOVA for the TLB disease and grain yield indicated that the source of variation for treatments, parents and hybrids was significant for all the traits under consideration



Fig. 2. The heat map represents the levels of resistance of maize parents and their hybrids to turcicum leaf blight disease based on AUDPC values. As indicated by the colour scale at the right of the heat map, low AUDPC values are represented by blue, medium AUDPC values by white, and high AUDPC values by red

Table 1. Mean values of	parental lines in res	pect of different parameters
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Parental lines	PDI (%)	AUDPC	Grain yield q/ha (Sick plot)	Grain yield q/ha (Naturel)	TLB reaction
IMIC 69	68.06ª	3050.00ª	19.83 ^{abc}	24.65 ^{bcd}	MS
IMIC 68	51.39 ^{ab}	2375.00 ^{ab}	36.75°	33.48 ^{abc}	MR
CI 4	65.28ª	2958.33ª	28.76 ^{ab}	43.04ª	MS
IMIC 02	52.78 ^{ab}	2400.00 ^{ab}	22.96 ^{abc}	31.69 ^{abc}	MR
IMIC 40	54.17 ^{ab}	2500.00 ^{ab}	20.76 ^{abc}	26.44 ^{bc}	MR
CTLB 01	31.94 ^b	1658.33 ^b	37.74ª	41.47 ^a	R
CTLB 02	30.56 ^b	1691.67 ^b	35.87ª	36.70 ^{ab}	R
CML 451	59.72 ^{ab}	2950.00ª	19.51 ^{abc}	28.17 ^{bc}	MS
CM 202	73.61ª	3325.00ª	8.17 ^c	13.15 ^d	MS
CM 111	77.78ª	3516.67ª	14.71 ^{bc}	22.43 ^{cd}	S
S.Ed.	5.46	229.48	7.06	2.21	-
CV	8.37	7.52	17.63	18.09	-

R=Resistant, MR=Moderately resistant, MS=Moderately susceptible, S=susceptible. The superscript lower case letters indicates significance value at 0.05 probability

e 2. Mean values of different parameters in F_1 hybrids

Hybrids	PDI (%)	AUDPC	Grain yield q/ha (Sick plot)	Grain yield q/ha (Naturel)	TLB reaction
IMIC-69 × IMIC-68	48.61 ^{fgh}	2183.33 ^{hijk}	44.59 ^{j-r}	56.72 ^{d-p}	MR
$IMIC-69 \times CI-4$	43.06 ^{jk}	1866.67 ^{no}	38.94 ^{p-t}	39.81 ^{k-p}	MR
$IMIC-69 \times IMIC-02$	41.67 ^{kl}	1875.00 ^{no}	62.91 ^{c-g}	58.37 ^{c-n}	MR
$IMIC-69 \times IMIC-40$	43.06 ^{jk}	1933.33 ^{mn}	37.19 ^{qrst}	38.58 ^{I-p}	MR
IMIC-69 × CTLB-01	48.61 ^{fgh}	2183.33 ^{hijk}	51.96 ^{g-m}	54.43 ^{e-p}	MR
IMIC-69 \times CTLB-02	48.61 ^{fgh}	2091.67 ^{ijkl}	62.59 ^{c-g}	70.95 ^{a-i}	MR
IMIC-69 × CML-451	47.22 ^{gh}	2116.67 ^{ijkl}	51.13 ^{h-n}	57.70 ^{c-o}	MR
IMIC-68 × IMIC-69	50.00 ^{fg}	2216.67 ^{hi}	72.26 ^{abcd}	83.04 ^{abc}	MR
$IMIC-68 \times CI-4$	48.61 ^{fgh}	2150.00 ^{ijk}	38.92 ^{p-t}	44.90 ^{h-p}	MR
$IMIC-68 \times IMIC-02$	41.67 ^{kl}	1825.00 ^{no}	53.80 ^{f-l}	53.77 ^{e-p}	MR
$IMIC-68 \times IMIC-40$	40.28 ^{Im}	1750.00 ^{opqr}	40.87 ^{m-t}	44.41 ^{i-p}	MR
IMIC-68 × CTLB-01	31.94 ^{qr}	1766.67 ^{opq}	40.84 ^{m-t}	47.23 ^{g-p}	R
IMIC-68 × CTLB-02	29.17 ^r	1541.67 ^{tuv}	30.49 ^t	31.21 ^{op}	R
IMIC-68 × CML-451	37.50 ^{mn}	1933.33 ^{mn}	47.53 ^{i-q}	51.89 ^{e-p}	MR
$CI-4 \times IMIC-69$	50.00 ^{fg}	2291.67 ^{gh}	39.57 ^{o-t}	44.45 ^{i-p}	MR
$CI-4 \times IMIC-68$	44.44 ^{ijk}	1925.00 ^{mn}	38.89 ^{p-t}	65.41 ^{a-k}	MR
$CI-4 \times IMIC-02$	52.78°	2425.00 ^{ef}	41.20 ^{m-t}	52.42 ^{e-p}	MR
$CI-4 \times IMIC-40$	50.00 ^{fg}	2208.33 ^{hij}	41.63 ^{m-t}	48.51 ^{f-p}	MR
$CI-4 \times CTLB-01$	38.89 ^{Imn}	1650.00 ^{q-u}	46.87 ^{i-q}	55.29 ^{d-p}	MR
$CI-4 \times CTLB-02$	36.11 ^{no}	1600.00 ^{stuv}	34.61 ^{rst}	52.74 ^{e-p}	MR
$CI-4 \times CML-451$	37.50 ^{mn}	1625.00 ^{r-v}	34.99 ^{rst}	42.63 ^{j-p}	MR
$IMIC-02 \times IMIC-69$	38.89 ^{Imn}	1741.67 ^{opqr}	43.97 ^{k-r}	43.80 ^{j-p}	MR
$IMIC-02 \times IMIC-68$	34.72 ^{op}	1650.00 ^{q-u}	45.36 ^{j-r}	42.10 ^{j-p}	MR
$IMIC-02 \times CI-4$	44.44 ^{ijk}	1833.33 ^{no}	55.61 ^{e-j}	52.42 ^{e-p}	MR Table continued

$IMIC-02 \times IMIC-40$	40.28 ^{Im}	1800.00 ^{nop}	45.24 ^{j-r}	48.51 ^{f-p}	MR
IMIC-02 × CTLB-01	40.28 ^{lm}	1750.00 ^{opqr}	57.53 ^{e-i}	63.84 ^{a-1}	MR
$IMIC-02 \times CTLB-02$	38.89 ^{Imn}	1675.00 ^{p-t}	63.44 ^{b-f}	86.41 ^{ab}	MR
IMIC-02 × CML-451	50.00 ^{fg}	2125.00 ^{ijkl}	42.79 ^{I-s}	42.74 ^{j-p}	MR
$IMIC-40 \times IMIC-69$	48.61 ^{fgh}	2200.00 ^{hijk}	47.80 ^{i-q}	51.53 ^{e-p}	MR
$IMIC-40 \times IMIC-68$	45.83 ^{hij}	2091.67 ^{ijkl}	44.14 ^{k-r}	88.22ª	MR
$IMIC-40 \times CI-4$	62.50 ^b	2866.67 ^{bc}	57.94 ^{e-i}	80.81 ^{abcd}	MS
$IMIC-40 \times IMIC-02$	48.61 ^{fgh}	2216.67 ^{hi}	61.31 ^{d-h}	86.56 ^{ab}	MR
IMIC-40 × CTLB-01	50.00 ^{fg}	2358.33 ^{fg}	65.55 ^{bcde}	86.12 ^{ab}	MR
$IMIC-40 \times CTLB-02$	62.50 ^b	2783.33°	51.33 ^{h-m}	71.23 ^{a-h}	MS
IMIC-40 × CML-451	56.94 ^c	2566.67 ^d	39.65 ^{n-t}	33.09 ^{nop}	MS
CTLB-01 × IMIC-69	37.50 ^{mn}	1600.00 ^{stuv}	47.08 ^{i-q}	36.12 ^{mnop}	MR
CTLB-01 \times IMIC-68	45.83 ^{hij}	2066.67 ^{kl}	43.99 ^{k-r}	49.31 ^{f-p}	MR
$CTLB-01 \times CI-4$	29.17 ^r	1508.33 ^v	56.81 ^{e-i}	57.94 ^{c-n}	R
$CTLB-01 \times IMIC-02$	29.17 ^r	1383.33 ^w	48.79 ^{i-q}	50.09 ^{e-p}	R
$CTLB-01 \times IMIC-40$	29.17 ^r	1650.00 ^{q-u}	54.8 ^{e-k}	51.19 ^{e-p}	R
$CTLB-01 \times CTLB-02$	30.56 ^{qr}	1591.67 ^{stuv}	71.14 ^{c-h}	72.83 ^{a-j}	R
CTLB-01 × CML-451	44.44 ^{ijk}	1933.33 ^{mn}	53.41 ^{f-l}	56.10 ^{d-p}	MR
$CTLB-02 \times IMIC-69$	40.28 ^{Im}	1741.67 ^{opqr}	49.36 ^{i-p}	43.80 ^{j-p}	MR
$CTLB-02 \times IMIC-68$	30.56 ^{qr}	1366.67 ^w	57.26 ^{e-i}	56.52 ^{d-p}	R
$CTLB-02 \times CI-4$	31.94 ^{qr}	1616.67	72.44 ^{abc}	73.78 ^{a-g}	R
$CTLB-02 \times IMIC-02$	30.56 ^{qr}	1533.33 ^{uv}	77.27ª	88.90ª	R
$CTLB-02 \times IMIC-40$	31.94 ^{qr}	1516.67 ^{uv}	73.82 ^{ab}	75.88 ^{a-e}	R
$CTLB-02 \times CTLB-01$	31.94 ^{qr}	1683.33 ^{pqrs}	70.67 ^{abcd}	72.25 ^{a-g}	R
$CTLB-02 \times CML-451$	34.72 ^{op}	1566.67 ^{stuv}	51.04 ^{h-o}	49.35 ^{f-p}	MR
CML-451 × IMIC-69	46.72 ^{hi}	2075.00 ^{jkl}	41.73 ^{m-t}	86.81ª	MR
CML-451 \times IMIC-68	53.67 ^{de}	2408.33 ^{efg}	41.56 ^{m-t}	34.26 ^{mnop}	MR
$CML-451 \times CI-4$	63.89 ^b	2916.67 ^b	38.12 ^{p-t}	60.91 ^{b-m}	MS
$CML\text{-}451\timesIMIC\text{-}02$	55.56 ^{cd}	2491.67 ^{de}	41.20 ^{m-t}	53.43 ^{e-p}	MS
$CML\text{-}451\timesIMIC\text{-}40$	52.78°	2508.33 ^{de}	34.54 ^{rst}	30.75 ^p	MR
CML-451 × CTLB-01	51.39 ^{ef}	2008.33 ^{Im}	43.69 ^{k-s}	55.86 ^{d-p}	MR
CML-451 × CTLB-02	50.00 ^{fg}	2008.33 ^{Im}	38.79 ^{p-t}	44.15 ^{j-p}	MR
RC (GH-150125)	32.22 ^{pq}	1533.33 ^{uv}	72.79 ^{abc}	74.88 ^{a-f}	R
SC (P-3507)	81.70ª	3866.67ª	32.45 st	80.48 ^{abcd}	S
S.Ed.	1.74	79.48	3.72	7.98	-
CV	3.46	3.50	6.42	12.63	-

R=Resistant, MR=Moderately resistant, MS=Moderately susceptible, S=susceptible. The superscript lower case letters indicates significance value at 0.05 probability

(Table 3), inferring that their existed sufficient variability for the TLB disease in terms of PDI and AUDPC values and so also for grain yield under sick plot and normal conditions. As a result, the analysis of combining ability and genetic parameters was further done using model I of Griffing's I design. The large variation among the parents and crosses in terms of TLB reaction and grain yield from the ANOVA indicated a high potential for breeding progress and yield increase.

A variance analysis of GCA and SCA was performed

by dividing the genetic variance into variance due to GCA and variance due to SCA (straight and reciprocal). The GCA variance of parents, SCA and reciprocal variances of cross combinations for all the traits are statistically significant (Table 5), indicating that both additive and non-additive gene interactions affecting the traits such as disease resistance and grain yield simultaneously (Badu-Apraku et al. 2021). The significance of reciprocal variance indicates the reciprocal effect involved in TLB resistance and grain yield. The results contradict most of the findings, which show no reciprocal effect on TLB resistance in maize (Sigulas et al. 1988, Schechert et al. 1997; Bucheyeki et al. 2017). Hence, there is a need to investigate maternal or cytoplasmic effects on TLB resistance in maize in different genetic backgrounds. On the other hand, reciprocal differences are reported for grain yield (Yerva et al. 2016; Onejeme et al. 2020). Therefore, selecting desirable male (pollen parent) and female (seed parent) parents is crucial when considering grain yield during hybridization.

Heritability can be estimated from the GCA and SCA effects and their variances when the combining ability differs significantly between crosses. The results of heritability showed that high broad sense and narrow sense heritability has been recorded by AUDPC (85.98 and 64.15) and PDI (90.18 and 63.51), indicating disease resistance for TLB could respond to phenotypic based selection (Carson 2006; Ayiga-Aluba et al. 2015). The ratio of $\sigma^2 A / \sigma^2 D$ is more than 1.0 for PDI and AUDPC, suggesting additive gene action is important in the inheritance of TLB disease resistance. These results are similar to those of previous studies of Ohunakin et al. (2020) and Abdelsalam et al. (2021) who found a preponderance of additive gene action in inheritance of TLB resistance in maize. Earlier, Sibiya et al. (2013) reported that both gca and sca were highly significant for both northern leaf blight and grain yield in maize and indicated the preponderance of additive over non-additive gene action for the traits in the inbred lines. The mean squares were also found highly significant in a study conducted by Nedi et al. (2018) in maize; they also emphasized the importance of both additive and non-additive gene interactions but they highlighted that predominantly the additive gene interaction is controlling the disease resistance.

Accordingly, the present findings suggested that TLB disease resistance in maize could eventually be increased through direct phenotypic selection or recurrent selection

(Hettiarachchi et al. 2009; Vivek et al. 2010). Whereas less than 1.0 of $\sigma^2 A / \sigma^2 D$ for grain yield under normal and sick plot conditions indicates that non-additive gene action plays an important role in genetic control of this trait. Likewise, low narrow sense heritability of grain yield also implied preponderance of non-additive gene actions in the inheritance (Patil et al. 2021; Suresh et al. 2021).

Baker's ratio was used to analyze the relative importance of GCA and SCA components in predicting progeny performance. Baker's ratios for PDI and AUDPC were higher than 0.5 and close to 1 (Table 4). Grain yield had a Baker's ratio that was less than 0.5 and close to zero. It indicates GCA component is relatively more important than SCA for disease resistance. Vivek *et al.* (2010) and Njoroge and Gichuru (2013) have also found the importance of GCA component in TLB resistance than SCA. Based on the prevalence of GCA components, it is clear that additive gene action is the major contributing factor of resistance to TLB in the inbred lines tested. It implies gca effects of inbred lines could effectively be utilized to predict hybrid performances for TLB resistance.

The general combining ability effect is important in selecting inbred lines to develop superior hybrids. The gca effects differed profoundly among parents (Table 5). The parent lines CTLB-02, CTLB-01 and IMIC-02 had gca effects in a negative direction for TLB disease PDI and AUDPC indicating that they are good combiners in desirable negative direction for TLB disease. This means that they are found to be promising for TLB disease resistance and can be used in crossing programme to develop TLB resistant hybrids. These findings are in accordance with Sibiya et al. (2013) and Badu-Apraku et al. (2021). Inbred line, CML-451 followed by IMIC-69 recorded highest gca effects for PDI and AUDPC in an undesirable positive direction inferring that these parental lines are towards TLB disease susceptibility. For grain yield CTLB-02 recorded highest *gca* effect in the desirable direction both under sick plot and normal situations indicating it to be a good combiner for grain yield, while, CML-451 recorded highest gca effect for grain yield in the undesirable negative direction under both conditions.

The negative gca effect for AUDPC and PDI is desirable for disease resistance. A parent with a high positive *gca* effect on grain yield would produce promising progeny. Accordingly, parents with both negative gca effects for disease severity and positive gca effects for yield are likely to produce high yields. Thus, comparisons of the *gca* values

Table 3. Analysis of variance (ANOVA) for eight parents and 501, hybrid.	Table 3. Analy	ysis of variance	(ANOVA) for	eight par	ents and 56 F	, hybrids
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Source of variation	df	PDI	AUDPC	Grain yield q/ha (Sick plot)	Grain yield q/ha (Naturel)
Replications	2	5.84	16416.02	32.32	149.49
Treatments	63	304.55**	535293.85**	598.68**	1068.46**
Parents	7	583.25**	891770.83**	193.04**	679.95**
Hybrids	55	247.35**	410294.85**	471.17**	821.90**
Error	126	281.15	6757.73	11.72	47.44

The symbols * and ** indicate significance at 0.05 and 0.01 probabilities, respectively.

						_
Source of variation df		PDI	AUDPC	Grain yield q/ha (Sick plot)	Grain yield q/ha (Natural)	
GCA	7	990.68**	953607.00**	805.76**	997.33**	
SCA	28	52.16**	41166.00**	225.62**	272.59**	
Reciprocal	28	38.07**	51387.00**	88.43**	239.55**	
Error	126	0.75	2271.00	1.26	15.18	
BSH		90.18	85.98	88.02	71.80	
NSH		63.51	64.15	27.19	10.06	
$\sigma^2 A / \sigma^2 D$		2.38	2.94	0.45	0.16	
Baker's ratio		0.70	0.75	0.31	0.35	

Table 4. ANOVA for combining ability to estimate mean of squares and genetic parameters

GCA= General combining ability, SCA=Specific combining ability, NSH=Narrow-sense heritability, BSH=Broad-sense heritability, σ_{2A} =Additive variance derived from GCA variance, σ_{2D} =Dominance variance derived from SCA variance. The symbols * and ** indicate significance at 0.05 and 0.01 probabilities, respectively

Tal	b	le 5.	General	comb	oining	ability	effects	of	[:] eight	parents
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Parental lines	PDI	AUDPC	Grain yield q/ha (Sick plot)	Grain yield q/ha (Natural)
IMIC 69	3.72 ^{ABab}	113.93 ^{Aabc}	-2.29 ^{Cbc}	-1.89 ^{CDb}
IMIC 68	0.24 ^{Cbcd}	-48.05 ^{Bbcd}	0.78 ^{BCab}	-1.23 ^{Db}
CI 4	1.84 ^{ABCab}	125.39 ^{Aabc}	0.25 ^{BCab}	2.65 ^{ABab}
IMIC 02	-3.63 ^{Dde}	-79.30 ^{Bcde}	0.74 ^{BCab}	1.75 ^{ABCab}
IMIC 40	0.88 ^{BCabc}	191.02 ^{Aab}	-1.00 ^{Cb}	0.85 ^{BCDab}
CTLB 01	-3.20 ^{Dcde}	-246.48 ^{Cde}	3.09 ^{ABab}	-0.38 ^{BCDb}
CTLB 02	-4.59 ^{De}	-293.36 ^{Ce}	5.89 ^{Aa}	4.98 ^{Aa}
CML 451	4.73 ^{Aa}	236.85 ^{Aa}	-7.45 ^{Dc}	-6.73 ^{Ec}
SE	0.31	16.85	0.40	0.92

Lowercase and uppercase letters indicate significance at 0.05 and 0.01 probabilities, respectively; SE= Standard error difference

for each parent and the trait showed that CTLB-02 to be a good potential parental line for both TLB disease resistance and grain yield.

The specific combining ability effects of 56 crosses are represented in Table 6. The sca effects for PDI for TLB and AUDPC values revealed that the cross between CTLB-01 \times CI-4 recorded highest sca effects in desirable negative direction followed by CTLB-01 \times IMIC-40 indicating that these are the best crosses for TLB disease only. From the previous section and Table 5, it is understood that the parental line CTLB-02 is said to be highly resistant for TLB disease followed by CTLB-01. However, the parental CTLB-01 is able to throw better TLB resistant hybrids in cross combination with male lines CI-4 and IMIC-40 as compared to CTLB-02 line. This may be due to better compensation of favourable alleles from both parents. For grain yield, the cross combination of CML-451 × IMIC-69 recorded the highest sca effects in a desirable positive direction under both sick plot and normal situation, followed by CML-451 imesCI-4 cross. In this case, even though CML-451 has recorded highest gca effects in undesirable negative direction for grain yield, but in cross combination with IMIC-69 and CI-4 which is of low × low gca cross is able to exhibit higher grain yield in F, hybrids, this may due to the interaction between poor alleles of the two parents.

Parental choice only on the basis of sca effect has limited value in breeding programs. Therefore, the sca effect should be combined with a high performance per se hybrid (Fashat et al. 2016). In that case the cross combination of CTLB-02 ×IMIC-40 was the best cross which recorded significant positive sca effects and higher grain yield under both sick plot and normal situation. Apart from this, the hybrid also had lower PDI And AUDPC for TLB disease. As per the opinion of Fashat et al. (2016) an ideal cross should have one off the parent with high *gca* effects, the above-mentioned cross is in line with the opinion wherein CTLB-02 is of high *gca* type for TLB and grain yield.

Some of the crosses showed resistant reaction to TLB along with high yielding ability suggesting the potentiality of newly generated hybrids, particularly, CTLB-02 × IMIC-02 and CTLB-02 × IMIC-40 which were highly resistant to TLB and also recorded maximum grain yield under both conditions (Table 3). These hybrids were the most promising among the test crosses based on the mean performance. Furthermore, resistant lines show less grain yield reduction under diseased condition when compared to moderately resistant and moderately susceptible crosses. The incidence and severity of *turcicum* leaf blight has increased in northern

Table 6.	Specific	combinina	ability e	ffects of F.	hvbrids
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Hybrids	PDI	AUDPC	Grain yield (q/ha) (Sick plot)	Grain yield (q/ha) (Natural)
$IMIC-69 \times IMIC-68$	0.31	92.84	-23.64	23.31
$IMIC-69 \times CI-4$	-6.84	-397.27	10.30	-4.44
$IMIC-69 \times IMIC-02$	-2.76	-184.24	0.65	4.51
$IMIC-69 \times IMIC-40$	-5.89	-396.22	-0.29	-1.52
IMIC-69 × CTLB-01	3.75	291.28	-3.46	-1.30
IMIC-69 × CTLB-02	5.14	246.48	-5.99	10.80
IMIC-69 × CML-451	-5.56	-258.72	-9.03	25.68
$IMIC-68 \times IMIC-69$	1.70	126.17	13.14	22.00
$IMIC-68 \times CI-4$	2.19	48.05	16.43	7.27
IMIC-68 × IMIC-02	0.71	-72.27	-12.85	0.05
$IMIC-68 \times IMIC-40$	-5.19	-417.58	-7.25	18.42
IMIC-68 × CTLB-01	-9.45	36.59	0.13	0.38
IMIC-68 × CTLB-02	-10.84	-141.54	3.81	-9.03
$IMIC-68 \times CML-451$	-11.81	-280.08	-11.74	-14.82
$CI-4 \times IMIC-69$	0.10	27.73	6.52	-13.53
$CI-4 \times IMIC-68$	-1.98	-176.95	11.17	-0.50
$CI-4 \times IMIC-02$	10.23	354.30	5.74	-3.24
$CI-4 \times IMIC-40$	2.94	-132.68	-8.30	9.01
$CI-4 \times CTLB-01$	-4.10	-253.52	-1.32	-4.04
$CI-4 \times CTLB-02$	-5.48	-256.64	-1.01	7.60
$CI-4 \times CML-451$	-13.41	-761.85	13.70	-3.89
$IMIC-02 \times IMIC-69$	-5.54	-317.58	-3.51	-2.78
$IMIC-02 \times IMIC-68$	-6.23	-247.27	-6.53	-5.93
$IMIC-02 \times CI-4$	1.89	-237.37	3.26	-1.44
$IMIC-02 \times IMIC-40$	-1.32	-336.33	5.77	7.17
IMIC-02 × CTLB-01	2.76	51.17	0.05	3.10
$IMIC-02 \times CTLB-02$	2.76	23.05	-0.04	33.79
$IMIC-02 \times CML-451$	4.56	-57.16	-12.79	-5.77
$IMIC-40 \times IMIC-69$	-0.33	-129.56	12.42	-7.00
$IMIC-40 \times IMIC-68$	0.36	-75.91	-6.19	14.26
$IMIC-40 \times CI-4$	15.44	525.65	-2.14	12.61
$IMIC-40 \times IMIC-02$	7.02	80.34	8.83	8.98
IMIC-40 × CTLB-01	7.97	389.19	-0.89	6.60
IMIC-40 \times CTLB-02	21.86	861.07	0.25	13.50
IMIC-40 \times CML-451	6.99	114.19	11.18	-20.13
$CTLB-01 \times IMIC-69$	-7.36	-292.06	8.93	-4.31
$CTLB-01\timesIMIC-68$	4.44	336.59	-25.29	-1.32
$CTLB-01 \times CI-4$	-13.82	-395.18	-1.82	2.02
$CTLB-01 \times IMIC-02$	-8.35	-315.49	-7.32	7.38

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CTLB-01 × IMIC-40	-12.86	-319.14	6.91	9.07
CTLB-01 × CTLB-02	-6.01	106.90	4.77	-3.05
CTLB-01 × CML-451	-1.43	-81.64	-7.12	1.40
CTLB-02 × IMIC-69	-3.20	-103.52	2.16	-2.94
CTLB-02 × IMIC-68	-9.45	-316.54	-1.48	-21.46
$CTLB-02 \times CI-4$	-9.65	-239.97	6.38	2.94
CTLB-02 × IMIC-02	-5.57	-118.62	-16.49	27.34
CTLB-02 × IMIC-40	-8.70	-405.60	17.51	5.23
CTLB-02 × CTLB-01	-4.62	198.57	19.00	-13.78
CTLB-02 × CML-451	-9.76	-401.43	7.33	-13.57
CML-451 \times IMIC-69	-6.06	-300.39	16.74	35.36
CML-451 \times IMIC-68	4.35	194.92	4.73	-3.82
CML-451 × CI-4	12.98	529.82	8.16	14.87
CML-451 \times IMIC-02	10.12	309.51	6.46	11.19
CML-451 \times IMIC-40	2.82	55.86	23.10	-4.97
CML-451 × CTLB-01	5.52	-6.64	-26.06	14.09
CML-451 × CTLB-02	5.52	40.23	6.63	9.85
S. Ed.	0.76	41.69	2.70	2.49

Karnataka and in few other areas where resistant parents showing some symptoms of susceptibility. Thus more resistant parents have to be identified and the genetics of resistance investigated to develop durable resistance.

Yan and Hunt (2002) showed significance of GGE biplot in diallel analysis. They explained genetic relation of germplasms used in the study by the vertexes of entries in polygon view. The gca and sca effects of the parents were examined by defining an Average Tester Coordinate (ATC). An average tester is defined as a virtual tester, of which PC1 and PC2 scores are equal to the average PC1 and PC2 scores, respectively, across all testers (indicated by block dot in Fig. 3). The ATC is established with its abscissa passing through the origin and average tester. The ordinate is drawn perpendicular to the ATC abscissa and passing through origin. Since, the gca and sca are orthogonal, ATC abscissa corresponds approximately to gca (i.e., vector of the average tester), and ATC ordinate corresponds approximately to sca (Yan 2001; Yan and Hunt 2002).

A total of 80.15 % variation was explained by PC1 (66.42 %) and PC2 (13.73 %) for per cent healthy plants. The biplot indicated CTLB-01 and CTLB-02 had highest gca effects, while IMIC-40 has the lowest *gca* effect for TLB resistance (Fig. 3).

The entry CI-4 and IMIC-68 had highest *sca* effect as they have largest projection onto the ATC ordinate, while CTLB-02 and CML-451 had smallest sca effects. An ideal tester is a highly representative tester (zero projection onto ATC

ordinate) and discriminative (longest vector). The IMIC-68 is coincided with the ideal tester; hence, it was the best tester with high discriminative ability for TLB resistance.

In addition, biplot describes the genetic background of



Fig. 3. Average tester ordinate view of biplot based on diallel data of eight parents which show different degrees of Turcicum leaf blight. Genotypes are labelled in upper-case letters when considered entries (female parent) and lower-case letters when observed as testers (male parent). A = IMIC-69, B = IMIC-68, C = CI-4, D = IMIC-02, E = IMIC-40, F = CTLB01, G = CTLB-02, H = CML-451. The block dot indicates Average Tester Coordinate (ATC)



Fig. 4. Polygon (Which won where) view of biplot based on diallel data of eight parents which show different degrees of resistance to Turcicum leaf blight. Genotypes are labelled in upper-case letters when considered entries (female parent) and lower-case letters when observed as testers (male parent). A = IMIC-69, B = IMIC-68, C = CI-4, D = IMIC-02, E = IMIC-40, F = CTLB01, G = CTLB-02, H = CML-451. The block dot indicates Average Tester Coordinate (ATC)

inbred lines resistant to TLB. IMIC-68 and IMIC-02, as well as CTLB-01 and CTLB-02, have similar types of alleles for disease resistance. As they are relatively close in biplot, it was assumed that they might have the same genetic makeup for TLB resistance. Hence, there is no heterosis between highly resistant parents CTLB-01 and CTLB-02. Similar results from GGE biplot analysis of diallel data were reported earlier by Dehghani et al. (2013) and Ghani et al. (2016). The CTLB-01 and CTLB-02 lines showed the strongest resistant reaction against TLB, which are promising for resistant breeding programmes.

The polygon view that the biplot is divided into six sectors, with entries IMIC-69, CI-4, IMIC-40, CTLB-01, CTLB-02 and CML-451 located on the vertex (Fig. 4) indicating the mating partners for TLB resistance. The lines IMIC-68, IMIC-69, CTLB-01 and CML-451 were present in sector CTLB-02 however, these crosses were not heterotic. Given that the CTLB-02 also exists in the CTLB-02 sector, the pure line (CTLB-02 x CTLB-02) would be the most effective among these crosses (Fig 4). In contrast, testers CI-4, IMIC-02 and IMIC-40 are present in the sector CTLB-01, the crosses CTLB-01 x [CI-4, IMIC-02, IMIC-40] are heterotic, since the CTLB-01 tester is not in the same sector (Fig 4). This is also evident from the mean PDI and AUDPC data in Tables 1 and 2.

In conclusion, there is a predominance of additive gene

action in controlling the TLB resistance of maize in this study. Highly significant GCA variance on disease incidence and AUDPC indicates the presence of additive gene action. This is further emphasized by additive to dominance ratio. Direct selection could, therefore, easily be practiced to improve TLB resistance in maize. As additive gene action dominates in TLB resistance, recurrent selection could be used to improve inbred lines for resistance, while non-additive gene action of grain yield could be exploited to develop resistant hybrids. Baker's ratio indicates that gca effects are more important than sca effects. Two parents CTLB-01 and CTLB-02 were identified as novel source of durable resistance for TLB. The GGE biplot showed CTLB-01 and CTLB-02 were genetically similar for disease resistance and IMIC-68 identified as ideal tester for disease resistance. CTLB-02 x IMIC-02 and CTLB-02 x IMIC-40 are best crosses for TLB resistance and also for grain yield.

Authors' contribution

Conceptualization of research (RMK); Designing of the experiments (RMK, GKN, IHS, SCT); Contribution of experimental materials (RZ, BJA, RMK); Execution of field/ lab experiments and data collection (BJA, RMK); Analysis of data and interpretation (BJA); Preparation of the manuscript (BJA, RMK, LPN, SCT).

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