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Generation mean analysis of Turcicum leaf blight resistance in maize

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Abstract

Turcicum leaf blight (TLB) caused by *Exserohilum turcicum* is an important disease of maize in India. Generation means analysis was undertaken to analyze the genetic basis of resistance to TLB, using parents, F_1, F_2, BCP_1 and BCP_2 generations of four different cross combinations of TLB resistant and TLB susceptible maize genotypes (Cross 1: CM138 x NAI147; Cross 2: CM139 x NAI147; Cross 3: CM139 x SKV18; Cross 4: CM139 x SKV21). Of these four, the first three were evaluated under artificial inoculation at UAS-ARS, Naganahalli (Karnataka) while the last was evaluated at VPKAS Farm at Hawalbagh (Uttarakhand) during *Kharif*-2008. Statistical analyses of the data, includes scaling test, joint scaling test and goodness-of-fit of generation means. Different models failed to fit the data for Cross 1 indicating presence of complex non-allelic interactions. Additive, additive x additive, additive x dominance and dominance x dominance genetic effects were important in the Cross 2. A model with additive, dominance, additive x additive, dominance x dominance effects best explained the genetic effects in Cross 3. Additive, additive x dominance and dominance x dominance effects were most important for expression of TLB in the Cross 4 at Hawalbagh. Thus, the analysis revealed that the nature of inheritance of TLB resistance could be population-specific. Although various types of gene effects were observed, the general tendency was predominance of additive genetic component, indicating that specific breeding procedures like recurrent selection could aid in improving TLB resistance.

Key words: Maize, Generation means analysis, Genetic effects, Turcicum leaf blight

Introduction

Among the biotic stresses affecting maize, the Turcicum leaf blight (TLB) disease (also known as Northern Corn Leaf Blight; NCLB), caused by *Exserohilum turcicum* (Pass) K.J. Leonard and E.G. Suggs [teliomorph: *Setosphaeria turcica* (Luttrell) Leonard and Suggs], is one of the most important in India. TLB disease is diseases of maize in particularly prevalent during *Kharif* (rainy) season in the Zones I, II and IV, as delineated by the AICRP (Maize), namely Peninsular, North eastern and Northern hill regions. Yield losses due to TLB worldwide can range from 27% to 90% [1,2] in addition to predisposing plants to stalk rots and reducing forage value. Utilization of host resistance is the most cost-effective and environmentally sound method of control of TLB [3, 4]. Also, studying the genetic basis of resistance is imperative in breeding for TLB resistance.

Generation mean analysis (GMA) is a relatively simple and statistically reliable tool suitable for preliminary estimation of various genetic effects [5]. Estimation and interpretation of non-allelic interactions are more progressive with generation mean analysis as it utilizes the first order statistics which are less compounded with each other when compared with variance estimates. Moreover, the populations evaluated in these studies can be utilized in actual breeding programmes.

In the present study, GMA for TLB resistance was undertaken using four crosses of maize, involving genetically divergent and phenotypically contrasting (with respect to TLB resistance/susceptibility) lines, to understand the genetic basis of resistance to TLB in each of the populations. The susceptible parental lines included CM138 and CM139, which are female parents of single-cross hybrids, Pusa Early Hybrid Maize-2 (PEHM2) and Parkash, respectively, and the resistant parental lines included NAI147, SKV18 and SKV21, which have been identified as sources of resistance to TLB in India in a separate study.

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Materials and methods

Six generations (P_1, P_2, F_1, F_2, BCP_1 and BCP_2) for each of the following four crosses, were evaluated in this study: Cross 1: CM138 (P_1) x NAI147 (P_2); Cross 2: CM139 (P_1) x NAI147 (P_2); Cross 3: CM139 (P_1) x SKV18 (P_2); Cross 4: CM139 (P_1) x SKV21 (P_2). The initial crosses were made at IARI Experimental Farm, New Delhi, during *Kharif* 2007. All the subsequent generations required for the study were developed during *Rabi* 2007-08 at Maize Winter Nursery, Hyderabad. Evaluation of the experimental materials, including all generations, was undertaken during *Kharif* 2008.

Various generations of the first three crosses (Cross 1, 2 and 3) were evaluated at UAS-ARS, Naganahalli (12°39'21"N, 76°15'36"E, 70 m.a.s.l), Karnataka in Zone 4, while the last cross was evaluated at VPKAS Experimental Farm, Hawalbagh (29°36'09.36"N, 79°39'10.00"E, 1234 m.a.s.l), Uttarakhand in Zone 1. At Naganahalli, for each of the three Crosses, the P_1, P_2 and F_1 constituted 4 rows each while F_2, BCP_1 and BCP_2 constituted 10 rows each with 20 plants per row. At Hawalbagh, the P_1, P_2 and F_1 comprised of 2 rows each, while the F_2, BCP_1 and BCP_2 comprised 10 rows each. Appropriate susceptible checks for TLB suitable for each location were sown after every 20th row to assess the disease pressure as well as to serve as spreader rows. TLB susceptible variety NAI219J was used as a check at Naganahalli, while CM212 served as a susceptible check at Hawalbagh.

Plants were artificially inoculated 25-30 days after seedling emergence. Local sources of inoculum were used at both locations for artificial inoculation. At Naganahalli, the infected leaf tissues were collected, sterilized with $HgCl_2$, washed thrice with sterile water, cultured on potato dextrose agar medium, and multiplied on sorghum seeds. For this, the sorghum seeds were soaked overnight, transferred to sterilized conical flasks next day, and the pathogen inoculum was added. The flasks were shaken once in two days, and equal amounts of fresh sorghum seeds were mixed after one week. The infected sorghum with pathogen inoculum were ground to fine powder, and 1–1.5g of the ground inoculum was added to each leaf whorl, followed by a light spray of water to moisten the tissue and initiate infection. The inoculation procedure was repeated twice at 10-day interval to ensure no disease escapes. At Hawalbagh, dried maize leaves infected with TLB were ground to powder and used as inoculum. The inoculation procedure was repeated thrice at one week interval to ensure no disease escapes. Standard agronomic practices, except for disease control, were followed.

The TLB disease severity was recorded during the flowering stage at both locations. A standard visual scale of 1 to 5, in which a score of '1' indicating least severity and '5' indicating highest severity, was utilized. Since intermediate ratings between two numbers (1.5, 2.5, 3.5 etc.) were also considered appropriate by the CIMMYT Pathologists, a modified rating scale (largely based on the CIMMYT TLB rating system) was adopted in this study. Genotypes with a score <2.5 were considered as 'resistant' (R); a score between 2.5-<3.0 as 'moderately resistant' (MR); a score between 3.0-<3.5 as 'moderately susceptible' (MS); and a score >3.5 as 'susceptible' (S).

GMA was undertaken using Windostat 8.0 Advanced Plant Breeding Package (Indostat Services, Hyderabad). A scaling test was performed to test the adequacy of additive-dominance model. The four scaling tests, as given by Hayman and Mather [6], were adapted as follows: $A = 2B_1-P_1-F_1$; $B = 2B_2-P_2-F_1$; $C = 4F_2-2F_1-P_1-P_2$; and $D = 2F_2-B_1-B_2$. Wherever the additive dominance model was inadequate, the Six Parameter Model of Hayman (1958) was used for estimation of various genetic components, where m = Mean, d = Additive effect, h = Dominance effect, i = Additive x Additive type of gene interaction, j = Additive x Dominance type of gene interaction, and l = Dominance x Dominance type of gene interaction.

The genetic parameters were also estimated using the joint scaling test [7]. Instead of testing the various relationships individually, the joint scaling test combines the full set of scaling tests into one. Since the six generation means to which the model was fitted was not known in equal precision, the generation means and their expectations were weighted using the reciprocals of the variance of means as the weight. Various generation means were predicted based on the parameters estimated and the test for goodness-of-fit was conducted using chi-square statistic. If the P value for the calculated chi-square (χ^2) was >0.05, the models were considered adequate. Different combinations of reduced number of parameters were tested in order to identify the best fitting model.

Results and discussion

High disease pressure was achieved through artificial inoculations at both locations, as was evident from the disease severity of susceptible checks used at the test

locations. Also, clear contrast in terms of TLB severity could be seen in the pairs of resistant and susceptible parents, especially at Naganahalli. The results obtained for different crosses are presented below.

Cross 1: The mean TLB scores of the six generations derived from the cross CM138 x NAI147 (Fig. 1) evaluated at Naganahalli are given in Table 1A. The mean of the different generations ranged from 1.16 in P_2 (NAI147) to 3.99 in F_2. While the mean of F_1 generation was intermediate of the two parents, the mean of the F_2 generation was higher, and lied out side the range of both parents. The parameter estimates for all the four scaling tests were highly significant indicating the inadequacy of additive/dominance model and the importance of gene interaction (Table 2A). The weighted joint scaling test conducted with only mean, additive and dominance effects in the model also failed to fit the expectations as indicated by a highly significant $\chi 2$ value. Out of several extended models with interaction effects, the parameter estimates for the best fitting model is given in Table 3A. However, this model with the parameters m, d, h, i and j also failed to fit the observed data for generation means as indicated by a highly significant $\chi 2$ value (Table 4). The inability of the models to fit the data in spite of inclusion of non-allelic interactions may be a result of unaccounted and complex interactions of factors influencing disease severity in the progenies of this specific cross.

Cross 2: The observed generation mean values for the cross CM139 x NAI147 at Naganahalli are given in Table 1B. The mean for different generations ranged from 1.11 in P_2 (NAI147) to 3.14 in P_1 (CM139). Parameter estimates for all four scaling tests were significantly different from zero indicating the inadequacy of additive/dominance model (Table 2B), which was further confirmed by the joint scaling test. A model with interaction components (but no dominance) fitted the observed values satisfactorily, as indicated by the non-significant $\chi 2$ value. All the components of the model, namely m, d, i, j and l were found to be significant (Tables 3B). Additive x dominance interaction effect was negative in value, while the rest of the parameters had positive values. The absence of dominance among genetic parameters emphasizes the need for adapting a breeding procedure that will fix the additive component in this cross.

Cross 3: The observed generation mean values for the cross CM139 x SKV18 ranged from 1.86 in P_2 (SKV18) to 3.32 in P_1 (CM139) (Table 1C). Parameters C and D in the scaling test were significant indicating the importance of non-allelic interactions, while A and B were not significant (Table 2C). Parameters C and D are considered as indicators of the importance of dominance x dominance and additive x additive types of interactions, respectively. The joint scaling test for the additive/dominance model also confirmed the need for considering allelic interactions in the model. A model with mean, additive, dominance, additive x additive,

Table 1. Generation means for TLB scores of different generations of the crosses evaluated at Naganahalli / Hawalbagh (*Kharif* 2008)

A. CM138 x NAI 147

Generation	Frequency	Mean	Variance	Var. of mean	Std. Error
P_1	50	3.46	0.294	0.006	0.077
P_2	55	1.16	0.139	0.003	0.050
F_1	56	1.96	0.581	0.010	0.102
F_2	150	3.99	0.195	0.001	0.036
BCP_1	145	3.68	0.343	0.002	0.049
BCP_2	147	1.82	0.421	0.003	0.054

B. CM139 x NAI 147

Generation	Frequency	Mean	Variance	Var. of mean	Std. Error
P_1	65	3.14	0.152	0.002	0.048
P_2	55	1.11	0.100	0.002	0.042
F_1	47	2.15	0.347	0.007	0.086
F_2	92	1.25	0.190	0.002	0.045
BCP_1	112	1.76	0.257	0.002	0.048
BCP_2	101	1.32	0.219	0.002	0.047

C. CM139 x SKV 18

Generation	Frequency	Mean	Variance	Var. of mean	Std. Error
P_1	47	3.32	0.353	0.075	0.087
P_2	29	1.86	0.552	0.020	0.138
F_1	40	2.30	0.369	0.009	0.096
F_2	134	2.13	0.427	0.003	0.057
BCP_1	130	2.87	0.177	0.001	0.037
BCP_2	133	1.95	0.414	0.003	0.056

D. CM139 x SKV 21

Generation	Frequency	Mean	Variance	Var. of mean	Std. Error
P_1	33	3.82	0.341	0.010	0.102
P_2	30	1.80	0.441	0.121	0.121
F_1	26	3.23	0.425	0.128	0.128
F_2	133	2.86	0.542	0.064	0.064
BCP_1	137	3.55	0.382	0.053	0.053
BCP_2	137	2.27	0.463	0.058	0.058

Fig. 1. Responses of (a) CM138 (P_1), (b) NAI147 (P_2), (c) BCP_1, (d) BCP_2 and (e) F_2 generations, to TLB in the trial at Naganahalli (*Kharif* 2008)

dominance x dominance effects best fitted the observations, as reflected by the non-significant $\chi 2$ value (Tables 3C). All the effects were significant and positive, except for dominance x dominance effect which had a negative value. Thus, a breeding procedure that will utilize both additive and dominance components, such as family selection with inter-mating, may be suitable for improvement of this population.

Cross 4: The observed generation mean values for the cross CM139 x SKV21, evaluated at Hawalbagh, are presented in Table 1D. The mean TLB scores ranged from 1.8 in P_2 to 3.82 in P_1. Scaling test indicated the significance of parameter B indicating the presence of non-allelic interactions (Table 2D). Joint scaling test also confirmed the importance of the same. A model with mean, additive, additive x dominance and dominance x dominance effects fitted the data best, as indicated by the non-significant χ^2 value (Table 3D). All the effects had significant and positive values. Thus, a breeding procedure that utilizes the additive variance effectively, such as family selection or recurrent selection, may suit the improvement of this population for the trait concerned.

Single-cross hybrids with their relatively uniform genetic constitution make them prime targets for devastating epidemics of the disease, particularly when both parents are susceptible. In a separate study (results not presented here), the inbred CM138 was found to be highly susceptible to TLB at Naganahalli, while CM139 was highly vulnerable to TLB at both Naganahalli and Hawalbagh. It is of significance that both these are elite female parents of two popular single-cross hybrids developed by public sector institutions in India. Therefore, there is a need for introgressing TLB resistance into these inbreds. Among the resistant genotypes used in these crosses, NAI147 is resistant to TLB at both locations; SKV21 is resistant to TLB at only Hawalbagh while SKV18 recorded resistance only at Naganahalli.

Generation mean analysis clearly revealed that the nature of inheritance could be population-specific. Therefore, appropriate breeding methods are to be adopted for the improvement of each population. Quantitative resistance is expressed independently of the physical environment and has never succumbed to TLB pathotypes in the field [4]. Ceballos *et al.* [8] after four cycles of full-sib S_1 recurrent selection in eight subtropical populations, primarily for improving polygenic resistance to TLB, obtained a 16% increase in resistance per cycle. They suggested high heritability and polygenic resistance to TLB. Highly heritable nature of polygenic resistance to TLB has been also reported by Ojulong *et al*. [9].

Table 2. Scaling test for TLB scores of different generations of the crosses evaluated at Naganahalli / Hawalbagh (*Kharif* 2008)

A. CM 138 x NAI 147

Parameter	Estimate	Variance	S.E. of mean	t value	P value
A	1.941	0.026	0.160	12.105	0.000
B	0.518	0.024	0.156	3.322	0.001
C	7.421	0.071	0.266	27.922	0.000
D	2.481	0.010	0.102	24.307	0.000

B. CM 139 x NAI 147

Parameter	Estimate	Variance	S.E. of mean	t value	P value
A	–1.770	0.019	0.137	–12.874	0.000
B	–0.624	0.018	0.134	–4.675	0.000
C	–3.545	0.067	0.258	–13.735	0.000
D	–0.576	0.013	0.113	–5.109	0.000

C. CM 139 x SKV 18

Parameter	Estimate	Variance	S.E. of mean	t value	P value
A	0.119	0.022	0.149	0.801	0.424
B	–0.267	0.041	0.202	–1.325	0.187
C	–1.274	0.114	0.338	–3.765	0.000
D	–0.563	0.017	0.131	–4.288	0.000

D. CM 139 x SKV 21

Parameter	Estimate	Variance	S.E. of mean	t value	P value
A	0.046	0.038	0.194	0.236	0.813
B	–0.491	0.045	0.211	–2.324	0.021
C	–0.621	0.156	0.394	–1.575	0.017
D	0.088	0.022	0.150	–0.588	0.557

Based on diallel analysis, Takamiya and Sendo [10] found that resistance to TLB was influenced by both additive and dominant gene effects. Their results showed that resistance was incompletely dominant. Carson [11] studying the inheritance of latent period length in maize infected with TLB through a generation mean analysis stated that over 92% of the generation means can be explained by additive gene action and recommended selection of some form based on the progeny mean. Hughes and Hooker [12] also conducted GMA for quantitative resistance to TLB and concluded that

Table 3. Joint scaling test for TLB scores of different generations of the crosses evaluated at Naganahalli / Hawalbagh (*Kharif* 2008)

A. CM 138 x NAI 147

Parameter	Estimate	Variance	S.E. of mean	t value	P value
m (Mean)	6.190	0.015	0.122	50.781	0.000
d (Additive)	1.121	0.002	0.046	24.539	0.000
h (Dominance)	4.562	0.040	0.201	22.701	0.000
l (Add. x Add.)	3.947	0.016	0.128	30.927	0.000
j (Add. x Dom.)	1.413	0.029	0.171	8.251	0.000

B. CM 139 x NAI 147

Parameter	Estimate	Variance	S.E. of mean	t value	P value
m (Mean)	0.946	0.003	0.057	16.597	0.000
d (Additive)	1.105	0.001	0.032	31.528	0.000
l (Add. x Add.)	1.177	0.005	0.068	17.263	0.000
j (Add. x Dom.)	–1.145	0.022	0.148	–7.726	0.000
l (Dom. x Dom.)	1.201	0.016	0.128	9.406	0.000

C. CM 139 x SKV 18

Parameter	Estimate	Variance	S.E. of mean	t value	P value
m (Mean)	1.354	0.072	0.268	5.094	0.000
d (Additive)	0.844	0.003	0.052	16.334	0.000
h (Dominance)	2.147	0.401	0.633	3.390	0.001
i (Add. x Add.)	1.187	0.068	0.260	4.558	0.000
l (Dom. x Dom.)	–1.200	0.171	0.414	–2.900	0.005

A. CM 139 x SKV 21

Parameter	Estimate	Variance	S.E. of mean	t value	P value
m (Mean)	2.794	0.002	0.049	57.444	0.000
d (Additive)	1.012	0.006	0.078	12.909	0.000
j (Add. x Dom.)	0.535	0.049	0.221	2.418	0.015
l (Dom. x Dom.)	0.424	0.023	0.150	2.822	0.005

additive, dominance and epistatic gene action were detected in specific populations. However, the importance of non-additive component was declared to be generally of minor importance when compared to additive gene action and variable with the population concerned. It was concluded that TLB resistance was conditioned by a relatively low number of genes, primarily additive in effect while recommending that breeding for resistance to TLB should be effectively accomplished by methods such as recurrent selection. The results obtained in the present study were, in general, congruent with the above findings. Shankaralingam *et al*. [13] suggested that additive gene action and dominance x dominance type of epistasis with duplicate nature are important in controlling resistance to TLB. Results from the GMA of CM139 x NAI147 cross confirmed the above finding.

Although various types of gene effects, namely additive, dominance and epistasis (i.e., additive x additive, additive x dominance and dominance x dominance) were observed in this study, the general tendency was for additive genetic component to be of predominant importance. The additive nature of resistance also emphasises the utility of procedures such as gene/QTL pyramiding to attain higher levels of resistance.

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Table 4. Goodness-of-fit test of generation mean estimates for TLB scores of different generations of the crosses evaluated at Naganahalli / Hawalbagh (*Kharif* 2008)

A. CM 138 x NAI 147

Generation	Weight	Observed	Expected	χ^2
P_1	169.90	3.460	3.365	1.548
P_2	394.57	1.164	1.123	0.667
F_1	96.47	1.964	1.628	10.906
F_2	770.86	3.993	3.909	5.459
BCP_1	422.61	3.683	3.836	9.958
BCP_2	349.54	1.823	2.009	12.039
			$\Sigma\chi^2$	40.576
			Probability	0.000

B. CM 139 x NAI 147

Generation	Weight	Observed	Expected	χ^2
P_1	426.50	3.139	3.138	0.000
P_2	555.61	1.109	1.109	0.000
F_1	135.49	2.149	2.147	0.000
F_2	485.33	1.250	1.247	0.006
BCP_1	436.35	1.759	1.762	0.004
BCP_2	462.00	1.317	1.320	0.004
			$\Sigma\chi^2$	0.014
			Probabilitv	0.906

C.CM139 x SKV18

Generation	Weight	Observed	Expected	χ^2
P_1	133.35	3.319	3.384	0.569
P_2	52.56	1.862	1.696	1.443
F_1	108.33	2.300	2.300	0.000
F_2	313.53	2.127	2.127	0.000
BCP_1	736.27	2.869	2.846	0.412
BCP_2	321.35	1.947	2.002	0.944
			$\Sigma\chi^2$	3.367
			Probability	0.067

D.CM139 x SKV21

Generation	Weight	Observed	Expected	χ^2
P_1	96.80	3.818	3.806	0.015
P_2	67.97	1.800	1.783	0.021
F_1	61.23	3.231	3.218	0.010
F_2	245.32	2.865	2.900	0.310
BCP_1	358.71	3.547	2.540	0.022
BCP_2	295.71	2.270	2.261	0.026
			$\Sigma\chi^2$	0.402
			Probability	0.818

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