



# Understanding the genetic architecture of resistance to northern corn leaf blight and southern corn rust in maize (*Zea mays* L.)

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(Received: October 2016; Revised: May 2017; Accepted: June 2017)

## Abstract

Among various foliar diseases, northern corn leaf blight (NCLB) incited by *Exserohilum turcicum* (Pass) Leonard and Suggs and southern corn rust (SCR) caused by *Puccinia polysora* (Underwood) are the most persistent and destructive biotic constraints in India and worldwide. The present investigation was conducted to understand the genetics of resistance to both diseases through six generation means and variances in two crosses developed by crossing two elite NCLB and SCR susceptible inbreds (CM212 and HKI162) with a common resistant inbred SKV50. Six generations of the two crosses (CM212 × SKV50 and HKI162 × SKV50) were evaluated in the disease screening nurseries for NCLB and SCR resistance at hot spot location during post rainy season of 2012 and 2013. The scaling tests and joint scaling tests indicated the inadequacy of additive-dominance model and showed the presence of epistatic gene effects in both the crosses for NCLB and SCR resistance. Study further revealed the importance of additive, dominance and additive × additive gene effects in the expression of NCLB and SCR. Duplicate gene interaction was evident in the inheritance of NCLB and SCR resistance in both the crosses. The study also revealed that genetic architecture of NCLB and SCR resistance was population specific. Both, additive and non-additive components were found important thus reciprocal recurrent selection would be more effective in developing NCLB and SCR resistant maize genotypes.

**Key words:** Generation means, additive-dominance model, duplicate gene interaction, recurrent selection

## Introduction

Maize (*Zea mays* L.) is one of the most important food crops worldwide along with rice and wheat, serving as staple food, livestock feed, and industrial raw material. Foliar diseases of maize are arguably the

primary biotic constraints to maize yields worldwide and the prevalence of these foliar diseases varies depending on the region or season (Smith 1999). In India, about 61 diseases have been reported to affect the crop (Payak and Sharma 1985). Among various foliar diseases, northern corn leaf blight and southern corn rust are regarded as the most persistent and destructive diseases of field maize.

Northern corn leaf blight (NCLB) incited by *Exserohilum turcicum* (Pass) Leonard and Suggs is a serious threat to maize cultivation worldwide causing yield losses of more than 50% (Raymundo and Hooker 1981; Perkins and Pederson 1987) and in India too, NCLB is the most important foliar diseases causing severe reduction in grain and fodder yield to the tune of 16-98% (Kachapur and Hegde 1988). The disease is prevalent in Karnataka, Andhra Pradesh, Bihar, Himachal Pradesh, Maharashtra and other regions. In Karnataka, NCLB has produced devastating effects in recent times and it causes reduction in grain yield of maize by 28-91% (Harlapur et al. 2000).

Southern corn rust (SCR) caused by *Puccinia polysora* (Underwood) is another major disease of maize in tropical and subtropical regions worldwide causing yield losses of up to 45-50% (Futrell 1975; Rodrigues et al. 1980). In India, southern corn rust was first noticed in 1991 in Bylukuppa of Mysore district and Arabhavi of Dharwad district in Karnataka (Payak 1994). Southern corn rust is considered most emerging disease in severe form with incidence of 45% in the North Karnataka (Harlapur et al. 2000) and yield loss of up to 50-70% (Agarwal et al. 2001). *Puccinia polysora* rust is becoming a major threat to maize crop

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in recent years, especially in southern Karnataka and adjoining states like Andhra Pradesh and Tamil Nadu.

Several disease management options have been recommended to reduce the impact of NCLB and SCR including conventional tillage, crop rotation, foliar fungicide application and planting of resistant hybrids. Among these practices, planting of resistant cultivars can effectively reduce the rate of disease development and is widely recommended. To breed a genotype with high level of resistance to NCLB and SCR, the knowledge of gene action involved in the expression of resistant reaction in the material being handled, is a pre-requisite to plan an appropriate breeding programme. Several researchers studied the inheritance of resistance to northern corn leaf blight (Hettiarachchi et al. 2009; Chaudhary and Mani 2010; Poland et al. 2011; Van Inghelandt et al. 2012; Ding et al. 2015; Cheng et al. 2016) and southern corn rust (Jines et al. 2007; Brewbaker et al. 2011; Wang et al. 2014) and suggested that resistance mechanism is complex and polygenic in nature.

Various biometrical approaches have been developed to decipher the genetic architecture and mode of inheritance of different characters related to yield. Generation mean analysis (Hayman 1958; Jinks and Jones 1958; Mather and Jinks 1971) is one such approach, which elucidates information about nature and magnitude of different gene actions viz., additive and dominance with an unambiguous test for epistasis. It also provides information about the type of epistasis viz., additive  $\times$  additive, additive  $\times$  dominance and dominance  $\times$  dominance operating in the inheritance of a character. Detection, estimation and interpretation of non-allelic interactions from generation mean analysis is statistically reliable as it is based on first order statistics which are less confounded with each other when compared with higher order statistics based estimates. Thus, the objective of this research program was to use the generation mean analysis to study the inheritance of resistance to NCLB and SCR in two maize populations to initiate breeding program to develop resistant inbreds.

## Materials and methods

### Plant material

Two susceptible inbreds CM212 and HKI162 were crossed with resistant inbred SKV50 through hand pollination during rainy season of 2011. During summer of 2011-12,  $F_1$  plants of both crosses were raised and selfed to produce  $F_2$  generation as well as backcrossed

to corresponding parents of each crosses to produce  $BCP_1$  [(CM212  $\times$  SKV50)  $\times$  CM212 and (HKI162  $\times$  SKV50)  $\times$  HKI162] and  $BCP_2$  [(CM212  $\times$  SKV50)  $\times$  SKV50 and (HKI162  $\times$  SKV50)  $\times$  SKV50] generations. Six generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BCP_1$  and  $BCP_2$ ) for each of the two maize crosses were tested for the disease response in the disease screening nurseries for northern corn leaf blight and southern corn rust at ZARS, V. C. Farm, Mandya during post rainy season of 2012 and 2013.

### Field layout for disease screening

The six populations of the two crosses were grown in a Randomized Complete Block Design with two replications. The non-segregating generations (parents and  $F_1$ s) were grown in four row plots of 2 meter length, while the segregating generations viz.,  $BCP_1$  and  $BCP_2$  were grown in ten row plots, and  $F_2$ s were grown in twenty row plots of 2 meter length. The entries were sown in rows spaced 75 cm apart and with an intra-row spacing of 20 cm. Appropriate susceptible checks for northern corn leaf blight (CM202 and NAI219J) and for southern corn rust (NAI219J) were sown after every 20<sup>th</sup> row to assess the disease pressure as well as to serve as spreader rows.

### Screening for resistance to northern corn leaf blight

To ensure uniform disease infestation, artificial inoculation was done by following the procedure given by Shekhar and Kumar (2012). The infected leaf tissues were collected from the diseased field, and washed thrice with sterile water, cultured on potato dextrose agar medium, and then 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 amount of fresh sorghum seeds were mixed after one week. The infected sorghum seeds with pathogen inoculum were ground to fine powder and 1 to 1.5 g of the ground inoculum was added to each leaf whorl, followed by a light spray of water to moisten the tissue and initiate infection. Artificial inoculation was made 20 days after sowing between 3.00 to 6.00 PM and inoculation was repeated twice after one week interval of first inoculation.

The northern corn leaf blight severity was recorded at flowering stage i.e., 60<sup>th</sup> day after sowing by visualizing the leaf area using a standard scale consisting of five broad categories designated by numerals from 1 to 5 (Payak and Sharma 1983). Since,

intermediate ratings between two numerals (1.5, 2.5, 3.5 and 4.5) (based on the CIMMYT northern leaf blight rating system) were also given and used in this study. Genotypes with a score <2.5 were considered as 'resistant'; score between 2.5-<3.0 as 'moderately resistant' (MR); score between 3.0-<3.5 as 'moderately susceptible' (MS); score 3.5-<4.0 as 'susceptible' (S) and score 4.0-5.0 as 'highly susceptible' (HS).

### Screening for resistance to southern corn rust

Artificial inoculation was done following the procedure suggested by Shekhar and Kumar (2012). The rust infected leaves were collected from severely diseased maize plots and were macerated thoroughly in between two palms of the hand dipped in the bucket of water, until the water got sufficiently colored. Inoculation for southern corn rust was made at 6 to 8 leaf stage and inoculation was repeated within two weeks. The spore (urediniospore) suspension @ 60, 000 spores/ml was applied in the leaf whorl using a sprayer in the early morning hours.

The southern corn rust severity was assessed at dough stage i.e., 80<sup>th</sup> day after sowing by visualizing the percentage leaf area covered by rust pustules on a rating scale of 1 to 5 (Cramer 1967) and intermediate ratings between two numerals was recorded as per Shekhar and Kumar (2012). Plants were classified based on the disease reaction as described above for northern corn leaf blight.

### Statistical analysis

Analysis of variance was conducted on phenotypic data using PROC GLM of SAS (version 9.3). Bartlett's

test was used to test for homogeneity between seasons before pooling the data (Gomez and Gomez, 1984). Components of variance were computed considering various effects (seasons, replicates, populations and seasons x populations) as random in the statistical model. To detect the presence or absence of epistasis, four scaling tests (A, B, C and D) of Mather (1949) were used. The six parameter model (Jinks and Jones 1958; Mather and Jinks 1971) was used to estimate gene effects when additive-dominance model was inadequate as indicated by joint scaling test of Cavalli (1952). Student t-tests were used to determine the significance of the estimated genetic parameters, and genetic components estimated to be different from zero at  $\alpha < 0.05$  were considered to contribute significantly to the model. The minimum number of effective factors differentiating the parents was worked out using the formula given by Wright (1968) and the potence ratio (PR) which indicates the degree of dominance was computed from generation means as per Peter and Frey (1966).

### Results and discussion

The means, variances, and variance of means of the six generations in the two crosses for reaction to northern corn leaf blight and southern corn rust are presented in Table 1. Analysis of variance revealed significant differences for seasons and populations for northern corn leaf blight and southern corn rust in the two crosses, indicating the existence of genetic variation and possibility of selection for resistant phenotypes. The population  $\times$  season interaction was also significant displaying differential response of populations in different seasons. Higher expression

**Table 1.** Six generation means with their standard error, variance and variance of mean for response to northern corn leaf blight and southern corn rust incidence during post rainy season of 2012 and 2013

Parents/generations	Northern corn leaf blight			Southern corn rust		
	Mean $\pm$ SE	Variance	Variance of mean	Mean $\pm$ SE	Variance	Variance of mean
Parents (40) CM212	3.713 $\pm$ 0.103	0.422	0.0105	3.288 $\pm$ 0.069	0.191	0.0048
HKI162	3.225 $\pm$ 0.074	0.217	0.0054	3.062 $\pm$ 0.082	0.272	0.0068
SKV50	0.888 $\pm$ 0.066	0.173	0.0043	0.475 $\pm$ 0.069	0.192	0.0048
F <sub>1</sub> s (40) CM212 $\times$ SKV50	2.488 $\pm$ 0.110	0.481	0.0120	2.075 $\pm$ 0.077	0.238	0.0059
HKI162 $\times$ SKV50	2.425 $\pm$ 0.092	0.340	0.0085	1.862 $\pm$ 0.064	0.166	0.0042
F <sub>2</sub> s (200) CM212 $\times$ SKV50	2.403 $\pm$ 0.070	0.969	0.0048	2.550 $\pm$ 0.062	0.759	0.0038
HKI162 $\times$ SKV50	2.715 $\pm$ 0.066	0.858	0.0043	2.337 $\pm$ 0.059	0.701	0.0035
BCP <sub>1</sub> (100) CM212 $\times$ (CM212 $\times$ SKV50)	3.335 $\pm$ 0.084	0.702	0.0070	3.030 $\pm$ 0.053	0.282	0.0028
HKI162 $\times$ (HKI162 $\times$ SKV50)	3.035 $\pm$ 0.071	0.501	0.0050	2.510 $\pm$ 0.051	0.257	0.0026
BCP <sub>2</sub> (100) SKV50 $\times$ (CM212 $\times$ SKV50)	1.975 $\pm$ 0.057	0.325	0.0033	1.750 $\pm$ 0.057	0.326	0.0033
SKV50 $\times$ (HKI162 $\times$ SKV50)	1.690 $\pm$ 0.081	0.650	0.0065	1.350 $\pm$ 0.070	0.492	0.0049

Figures in parenthesis indicate sample size

of the northern corn leaf blight and southern corn rust severity was observed in both segregating and non-segregating generations ( $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ,  $BCP_1$  and  $BCP_2$ ) of the crosses ( $CM212 \times SKV50$  and  $HKI162 \times SKV50$ ) due to artificial inoculation and favourable environmental conditions in both environments. Wide variation in NCLB and SCR disease severity scores was observed among non-segregating populations and the severity score was maximum in the susceptible parent (Fig. 1), while the  $F_1$ s recorded intermediate



**Fig. 1.** Reaction of the parents SKV50 and CML153 to Northern corn leaf blight (NCLB) and Southern corn rust (SCR) at ZARS, Mandya

NCLB and SCR score compared to the corresponding parents indicating quantitative nature of disease resistance. The mean of  $F_1$  generation was intermediate of the two parents in the earlier studies also (Hettiarachchi et al. 2009; Ishfaq et al. 2014). Quantitative nature of these two diseases is in accordance with previously published results of (Brewbaker et al. 2011; Wang et al. 2014; Ding et al. 2015; Cheng et al. 2016; Olukolu et al. 2016). Among

segregating generations, the disease score of  $BCP_1$  population of both crosses was maximum compared to either  $BCP_2$  or  $F_2$  populations. It has clearly established that parents selected for the study were highly diverse in their disease severity. Probably because of diverse nature of the parents, even  $F_2$  and backcross generations also exhibited a wide range in their reaction to NCLB and SCR incidence.

The mean and variance of NCLB and SCR disease scores in six generations of both crosses were subjected to Mather's scaling tests and Cavalli's joint scaling test to check the presence or absence of gene interactions in the inheritance of these traits (Table 2). Both scaling tests and joint scaling test were significant in both crosses which indicated the inadequacy of simple additive-dominance model in explaining the observed variation in the generation means for NCLB and SCR resistance thereby justifying the use of six parameter model for detection of interaction. This kind of inadequacy of additive-dominance was reported by other workers also (Barakat et al. 2008; Hettiarachchi et al. 2009). The highly significant mean effects [ $m$ ] for both diseases in the two crosses also indicated that disease reaction is quantitatively inherited. After ascertaining the failure of additive-dominance model, a perfect fit solution (Mather and Jinks 1971) was fitted to estimate the magnitude and direction of digenic interaction effects for the two crosses (Table 3).

### Gene effects

#### Northern corn leaf blight

The additive [ $\hat{d}$ ], dominance [ $\hat{h}$ ], additive  $\times$  additive [ $\hat{i}$ ] interaction gene effects were significant and positive in both the crosses of maize while dominance  $\times$  dominance [ $\hat{l}$ ] interaction effect was significant in

**Table 2.** Scaling tests and test for adequacy of additive-dominance model for the inheritance of resistance to northern corn leaf blight and southern corn rust

Disease	Cross	Scaling tests							$\chi^2$ value
		A	B	C	D	[ $m$ ]	[ $\hat{d}$ ]	[ $\hat{h}$ ]	
Northern corn leaf blight	CM212 $\times$ SKV50	0.470* $\pm$	0.275 $\pm$	-0.265 $\pm$	-0.505** $\pm$	2.486** $\pm$	1.273** $\pm$	0.105 $\pm$	78.58**
	HKI162 $\times$ SKV50	0.225	0.176	0.377	0.172	0.058	0.054	0.114	
	HKI162 $\times$ SKV50	0.420* $\pm$	0.068 $\pm$	1.898** $\pm$	0.705** $\pm$	2.132** $\pm$	1.205** $\pm$	0.547** $\pm$	
Southern corn rust	CM212 $\times$ SKV50	0.184	0.197	0.335	0.169	0.046	0.045	0.094	22.13**
	CM212 $\times$ SKV50	0.698** $\pm$	0.662** $\pm$	2.000** $\pm$	0.320* $\pm$	2.195** $\pm$	1.250** $\pm$	0.230** $\pm$	
	HKI162 $\times$ SKV50	0.148	0.161	0.310	0.146	0.048	0.045	0.090	
	HKI162 $\times$ SKV50	0.095 $\pm$	0.363* $\pm$	2.088** $\pm$	0.815** $\pm$	1.880** $\pm$	1.263** $\pm$	0.165* $\pm$	99.12**
	SKV50	0.146	0.169	0.290	0.147	0.046	0.045	0.083	

\*Significant at 5% level of significance, \*\*Significant at 1% level of significance

the cross CM212 x SKV50. Hettiarachchi et al. (2009) also reported additive, additive x additive and dominance x dominance genetic effects for resistance to NCLB. Although, additive and additive x additive gene effects were significant, non-additive gene effects appeared to overpower them in the inheritance of NCLB thereby indicating the utilization of breeding procedures that utilize both additive and dominance components. The observed differences in the crosses could be attributed to change in gene frequencies and proportion of dominance and recessive genes possessed by parents (Viana et al. 1999). Several researchers (Hettiarachchi et al. 2009; Chaudhary and Mani 2010; Njoroge and Gichuru 2013; Ishfaq et al. 2014) also reported both additive as well as non-additive gene action in the expression of resistance to NCLB. Duplicate gene interaction based on the significant opposite signs of  $[\hat{h}]$  and  $[\hat{l}]$  components was involved in the genetic control of NCLB in both crosses (Hettiarachchi et al. 2009). The duplicate epistasis generally hinders the improvement through selection and also placing a limitation on exploitation of higher magnitude of dominance and dominance x dominance gene effects (Jain et al. 1988). However, significant role of dominance variance along with duplicate epistasis in the inheritance of resistance favours the development of single cross hybrids (Patil et al. 2016).

**Southern corn rust**

Preponderance of additive gene effect  $[\hat{d}]$  and additive x additive interaction effect  $[\hat{i}]$  was observed in the inheritance of SCR incidence in the cross CM212 x SKV50. Non-significance of dominance gene effect need not necessarily mean that dominance is completely absent, because such results may be obtained due to cancellation of dominance gene effects at various loci. The present results are in agreement with the findings of Vieira et al. (2011). Thus, family selection or recurrent selection procedures that utilize the additive variance effectively may be used for the improvement of this population. In the cross HK1162 x SKV50, both additive and non-additive gene effects were significant and found to be imperative in SCR incidence (Brewbaker et al. 2011; Qing et al. 2016). Breeding strategies exploiting both additive and dominance components such as family selection with intermating, may be suitable for improvement of this population. The operation of duplicate type of epistasis in the inheritance of SCR was noticed in both the crosses (Brewbaker et al. 2011) and it moderates the variability range in the population thereby limiting the response to selection.

**Table 3.** Components of gene effects based on perfect fit solutions (Joint Scaling Test), number of effective factors and potence ratio (in F<sub>1</sub> and F<sub>2</sub>) for northern corn leaf blight and southern corn rust

Disease	Cross	[m]	[\hat{d}]	[\hat{h}]	[\hat{i}]	[\hat{j}]	[\hat{l}]	Type of epistasis	No. of effective factors (N) in F <sub>2</sub>	Potence ratio in F <sub>1</sub>	Potence ratio in F <sub>2</sub>
Northern corn leaf blight	CM212x SKV50	1.440**±	1.263**±	2.803**±	1.010**±	0.195±	-1.755**±	Duplicate	2.06	0.13	0.15
	HK1162x SKV50	0.350	0.064	0.854	0.344	0.240	0.554	Duplicate	1.38	0.32	1.13
Southern corn rust	CM212x SKV50	3.466**±	1.169**±	-1.964**±	-1.410**±	0.353±	0.922±	Duplicate	1.92	0.14	0.95
	HK1162x SKV50	0.342	0.049	0.848	0.339	0.236	0.545	Duplicate	1.57	0.07	0.88

\*Significant at 5% level of significance, \*\*Significant at 1% level of significance

Minimum number of effective factors influencing the trait in  $F_2$  generation and the degree of dominance computed from generation means of  $F_1$  as well as  $F_2$  generation in terms of potence ratio for the two crosses (CM212  $\times$  SKV50 and HKI162  $\times$  SKV50) for northern corn leaf blight and southern corn rust were estimated (Table 3). In both crosses, NCLB and SCR resistance was under the control of one group or two groups of effective factors. Several studies (Hettiarachchi et al. 2009; Brewbaker et al. 2011) also revealed that resistance to northern corn leaf blight and southern corn rust was conditioned by relatively less number of genes. Potence ratio in  $F_1$  and  $F_2$  generation of both crosses revealed the preponderance of partial dominance in the genetic control of resistance to NCLB and SCR (Brown et al. 2001; Wanlayaporn et al. 2013; Ding et al. 2015). These results were in accordance with disease expression in the  $F_1$ s and  $F_2$ s in both crosses against *Exserohilum turcicum* and *Puccinia polysora* infection in this study.

It is interesting to know whether there is overlapping or positional correspondence of genomic regions for these two economically important foliar diseases as genetic dissection of chromosomal regions putatively associated with multiple disease resistance will allow introgression of resistance genes in biparental segregating populations. Welz et al. (1999) found strong evidence for the association of loci for resistance to NCLB and common rust. However, Jiang et al. (1999) found no positional correspondence between the genomic regions identified for resistance to NCLB and common rust. Even Brown et al. (2001) reported that QTLs for NCLB and common rust were unlinked.

Overall the present investigation involving six generation mean analysis revealed that the genetic architecture of resistance to northern corn leaf blight and southern corn rust was population specific. Hence breeding methods to be adopted for the improvement of each population needs to be different. Both additive and non-additive components were found important for NCLB and SCR resistance, hence recurrent selection programmes are appropriate to develop improved resistant inbred lines first and then exploit disease resistance in  $F_1$ s (Ceballos et al. 1991; Hettiarachchi et al. 2009; Ayiga-Aluba et al. 2015; Ribeiro et al. 2016; Abadassi 2016).

#### Authors' contribution

Conceptualization of research (HCL); Designing of the experiments (HMR, HCL); Contribution of experimental materials (HMR, HCL); Execution of field/lab

experiments and data collection (HMR, HCL); Analysis of data and interpretation (HMR, HCL); Preparation of manuscript (HMR, HCL, ASP).

#### Declaration

The authors declare no conflict of interest.

#### Acknowledgement

The authors gratefully acknowledge the financial support provided by M/s. Pioneer Hi-Bred Seeds Pvt. Ltd., Bengaluru, to conduct experiments.

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