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Genetic analysis of resistance to post flowering stalk rot in tropical germplasm of maize (*Zea mays* L.)

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ABSTRACT

Post flowering stalk rot (PFSR) is one of the major biotic constraints to maize production in tropical and sub-tropical environments. It is a complex disease caused by multiple pathogens, among which *Fusarium moniliforme* and *Macrophomina phaseolina* are the major ones that cause severe yield losses in the Asian tropics. A set of maize inbred lines was evaluated at two locations for Fusarium stalk rot (FSR) and Macrophomina stalk rot (MSR). Based on line evaluation trials, resistant and susceptible lines were selected and crossed following a Diallel mating design IV to study the gene action for resistance to these stalk rots and the estimating the combining ability of inbred lines. A 9 × 9 diallel (Diallel-A) produced 36 hybrids for studying FSR resistance, and a 12 × 12 diallel (Diallel-B) produced 66 hybrids to analyse the resistance towards both FSR and MSR. These hybrids were evaluated at two locations for MSR and one location for FSR with artificial inoculation. The hybrids differed significantly for FSR ($p < 0.05$), as was the general combining ability (GCA) effects ($p < 0.01$), while Specific combining ability (SCA) effects were found to be non-significant. The analysis of the trials under MSR, showed significant difference for GCA, SCA, GCA × environment ($p < 0.01$), and hybrid × environment ($p < 0.05$) while SCA × environment was non-significant. The Baker ratio, which shows the relative importance of GCA over SCA, was close to unity for both the stalk rots, and hence a predominant additive gene effect was inferred towards resistance to these diseases. Though the GCA × environment interaction was significant for MSR, this study identified lines and their cross combinations with high resistance and large GCA and SCA effects across environments for FSR and MSR This offers scope for source population improvement for resistance to these stalk rots, as well as developing maize hybrids with stable resistance to Post flowering stalk rot.

1. Introduction

Maize has the highest global production among cereals. In Asia, eight major maize growing countries - China, India, Indonesia, Nepal, Pakistan, Philippines, Thailand and Vietnam produce 98 per cent of Asia's maize and 28 per cent of the global maize (Prasanna, 2014). Despite its impressive growth in Asia, the demand for maize in the developing world will be doubled by 2050 (Shiferaw et al., 2011; Rosegrant et al., 2009). Some of the major constraints that hinder maize production across the world are diseases, and in Asia, losses due to diseases range from 12% to 80% (Mahuku, 2010). Maize grown in the Asian tropics, especially during the wet season, is particularly vulnerable to an array of diseases, including downy mildews, leaf blights, rusts, stalk rots and ear rots.

Stalk rot is a serious biotic constraint in all parts of the world, including America, Australia and Europe. In Asia, PFSR is reported from all major maize growing countries, including Cambodia, China, India, Indonesia, Laos, Pakistan, Philippines, Thailand and Vietnam (Lal and Singh, 1984; Yang et al., 2010). Stalk rot is caused by different fungal pathogens and secondary colonizers (Afolabi et al., 2008). Fusarium stalk rot (FSR), Macrophomina stalk rot (MSR) and Late wilt are more prevalent and destructive in the Asian tropics (Khokhar et al., 2014). Estimated loss due to FSR in the rain-fed northern, central and southern regions in India is as high as 38 per cent (AICRP, 2014). MSR is reported to affect the maize crop in the drier regions of India, where the yield reduction due to MSR is estimated to be 63.5 per cent (Desai and Hegde, 1991).

PFSR is a complex disease and difficult to characterize, because a number of fungi may be involved in the decay of the pith, along with

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secondary infection by bacteria and nematodes (Khokhar et al., 2014). The disease is more prevalent when there is scarcity of irrigation especially after post flowering stage of the crop growth. It reduces yield directly by affecting various physiological pathways of maize plants that result in pre-mature lodging, which is the key cause of economic losses (Ledencan et al., 2003). The stalk rot pathogens thrive on good vegetative stage growth followed by stresses like drought, nutrient deficiencies, foliar diseases, insect and hail damage, high heat and prolonged cool and cloudy weather after flowering (Dodd, 1980). In general, stalk rot is more severe and show high incidence with increased fertilization of soils; potash fertilizers have been known to reduce severity whereas nitrogen increases disease incidence (Abney and Foley, 1971). Increase in plant population increases disease severity and incidence, especially in susceptible entries (White, 1999). Since there is a possibility of infection with multiple stalk rot pathogens, and strong interaction with crop management practices and environmental conditions, it has been a challenge to breed for stable resistance to PFSR. FSR and MSR are two of the most wide-spread stalk rots in the Indian sub-continent.

FSR caused *by Fusarium moniliforme,* is a non-obligate parasite and one of the most common reported fungi associated with maize crop. The *Fusarium* species causes seedling disease, root and crown disease, stalk rot and ear rot on maize (Cotten and Munkvold, 1998). *F. moniliforme* also produce mycotoxins like fumonisins that are the most common toxins found in diseased and symptomless maize kernels (Nelson et al., 1993). Fusarium species can survive at least for 360 days in surface or buried maize residues and can be a major source of inoculum (Cotten and Munkvold, 1998). FSR is a systemic disease which starts from the roots, spreading to the aerial plant parts and progresses to the upper internodes after flowering, causing the disintegration of pith tissues. Infected stalks show whitish pink to salmon discolouration of pith and vascular strands. This result in dryness of the plants, weakening of the stalk and eventually plant lodging, leading to severe yield losses (Sharma et al., 1993; Sibale et al., 1992).

MSR caused by *Macrophomina phaseolina* is an important soil borne fungus having a wide host range. It infects root and lower stem of over 500 plant species including maize (Kaur et al., 2012). It is more prevalent under high soil temperature and low moisture conditions, and can survive for more than 10 months under dry soil conditions (Khan, 2007). Microsclerotia produced in the infected roots and stem tissues of the host serves as a primary source of inoculum; Microsclerotia have been reported up to the depth of 0–20 cm in soil but are generally found in clusters on the soil surface (Alabouvette, 1990). The mode of infection of *Macrophomina phaseolina* is similar to that of *Fusarium moniliforme*. MSR is characterized by the presence of numerous, minute black sclerotia, particularly on vascular bundles and inside the rind of the stalk causing the stalk to appear greyish black. Higher application of nitrogen fertilizer and high plant densities also increase the severity of charcoal rot (Mughogho and Pande, 1984).

Asian maize germplasm has some sources of resistance for prevalent stalk rots, in the form of resistant inbred donor lines and populations/pools, nevertheless, the likelihood of more virulent strains and changing climate pose major challenges to the longevity of resistance. Host-plant resistance breeding programs require close surveillance of changes in virulence in existing pathogens and the identification or development of new resistant sources to new virulent strains (Zaidi et al., 2014). Development of disease resistant maize hybrids require an understanding of the gene action and combining ability of the inbred lines (GCA) and the cross combinations (SCA). Various mating designs, including diallel mating designs (Hallauer. et al., 2010) are important tools towards this end. Genetic studies of stalk rots caused by various pathogens by several research groups revealed that additive, non-additive and epistatic interactions are important for inheritance of resistance (Lunsford et al., 1976; Donahue et al., 1989; Singh and Kaiser, 1991; Santiago et al., 2010 and Krishna et al., 2013). High environmental variation was also observed in some of these studies, therefore the severity of the disease tends to vary with locations or environments resulting in significant genotype x environment (G x E) interaction. There have been reports of population improvement for resistance to stalk rots in maize through S_1 family selections or full-sib family selections (Khan and Paliwal, 1980) and through recurrent selection for GCA (Jinahyon and Russell, 1969). Improvement of the tropical Asian maize germplasm requires more concerted efforts towards developing and deploying varieties and hybrids with resistance to PFSR. Towards this objective, the present study was devised to analyse the gene action towards resistance to FSR and MSR, which are the major stalk rots in the Asian region. This study will also help to estimate combining abilities in a set of tropical maize inbred lines and hybrids, and their interaction with environment, to form the basis for defining breeding strategies to improve resistance to these diseases in CIMMYT-Asia's maize germplasm and further develop stalk rot resistant hybrid maize for Asia.

2. Materials and methods

2.1. Study sites

Tropical maize germplasm from International Center for Maize and Wheat Improvement (CIMMYT), Asia was evaluated for resistance to two stalk rots, FSR and MSR. FSR evaluation under artificial inoculation conditions was conducted at a hotspot location of Udaipur, Rajasthan at Maharana Pratap University of Agriculture & Technology (MPUAT) (25.46°N; 75.09°E; 577 masl; 633mm/year average annual rainfall) and at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) farms, Hyderabad (17.53° N; 78.27° E.; 545 masl; 784 mm/year average rainfall) during the rainy seasons (kharif) of 2011 and 2012. Hotspot locations have the favourable environments for disease development when a susceptible host genotype and adequate pathogen pressure are available. For MSR, inbred lines were evaluated under artificial inoculation at ICRISAT and Professor Jayashankar Telangana State Agricultural University (PJTSAU) farms, Hyderabad during the dry (Rabi) season of 2011. Hybrids were evaluated at Borlaug Institute for South Asia (BISA) farms at Ludhiana (30°55′ N, 75°54' E; 229 masl; 750–800 mm/year rainfall) and ICRISAT farms, Hyderabad for FSR and MSR under artificial inoculation conditions.

2.2. Maize germplasm

Three line evaluation trials were conducted for FSR. Line evaluation trial 1 (LET 1) with 85 tropical inbred lines was conducted at two locations; MPUAT, Udaipur and ICRISAT, Hyderabad. LET 2 with 92 tropical inbred lines was conducted at one location in MPUAT, Udaipur and LET 3 with 110 tropical inbred lines was conducted at ICRISAT, Hyderabad. MSR evaluation trial LET 4 with 105 tropical inbred lines was conducted on ICRISAT and PJTSAU farms, Hyderabad during the dry (Rabi) season of 2011 (Sup. Table 1). Inbred lines showing consistently low disease scores (≤ 5) across locations and years for either FSR or MSR were used as respective resistant parental lines, while lines exhibiting high disease scores (> 5) were used as susceptible parental lines for a diallel analysis.

2.3. Mating design and evaluation

Diallel mating design IV was used to study gene action and combining ability. A 9 × 9 diallel (Diallel-A) was formed with 9 inbred lines, which included 4 resistant, 2 moderately resistant and 3 susceptible parents for FSR, to develop 36 direct cross combinations (Sup. Table 2). Another diallel (Diallel-B) was formed with 12 inbred lines, which included 8 resistant and 4 susceptible lines to FSR and 6 resistant and 6 susceptible for MSR, resulting in 66 direct cross combinations (Sup. Table 3). Cross combinations were developed during the dry season of 2012 at ICRISAT farms, Hyderabad. All hybrids developed from Diallel-A along with three commercial hybrid checks 30V92 and P3396 from PHI Seeds Pvt. Ltd., and DKC8101 from Monsanto India

Ltd., were evaluated for FSR at two hotspot locations of BISA, Ludhiana and ICRISAT, Hyderabad farms, during the rainy season of 2013 under artificial inoculation conditions. Hybrids generated from Diallel-B along with two commercial hybrid checks, P3396 and DKC8101, were evaluated for FSR at two locations, BISA, Ludhiana and ICRISAT, Hyderabad, during the rainy season of 2013 under artificial inoculation conditions. For MSR evaluation, hybrids of Diallel-B along with commercial checks were planted at BISA, Ludhiana during the rainy season of 2013, and at ICRISAT, Hyderabad during the dry season of 2013 under artificial inoculation conditions.

2.4. Experimental design and layout

All the inbred and hybrid evaluation trials were planted in ALPHA-lattice design with two replications of single 3.0 m long rows with a spacing of 0.75 m between rows and 0.20 m between plants. In all the trials, 60 kg nitrogen per hectare in the form of urea, 60 kg/ha of phosphorous as single super phosphate, 40 kg/ha potassium as a muriate of potash, and 10 kg of zinc as zinc sulphate were applied as basal dose. Second and third doses of N (each 30 N kg/ha) were given as top dressing when the plants were about knee-high and at tasseling, respectively.

2.5. Inoculum preparation and inoculation technique

The trials were conducted under artificial inoculation using the toothpick method, which is the most used method, primarily because of the ease of multiplication of inoculum and rapidity of inoculation (Lal and Singh, 1984). Cultures of *F. moniliforme* and *M. phaseolina* were grown separately on wooden toothpicks to inoculate the test entries following the method suggested by Jardine and Leslie (1992), with slight modifications. To develop the inoculum, the toothpicks were soaked in distilled water overnight to remove toxic substances and then air dried. Approximately 250 toothpicks were packed in 250 ml glass bottles and a small quantity of distilled water (15 ml) was added to them before being autoclaved at 15 lbs and 121 °C for 15 min. After cooling the bottles, the distilled water was decanted and potato dextrose broth (PDB) was added into them and again autoclaved at the same temperature and pressure. Once the bottles were cooled, excess PDB was decanted aseptically and freshly cultured fungi were inoculated into the bottles. The inoculated bottles were incubated at 25 °C till the fungi had grown all around the toothpicks (for approximately 15 days).

Individual plants were inoculated by inserting the toothpicks colonized with either of the fungi, according to stalk rot under evaluation, into the second internode (first elongated node) of the plant at tassel emergence stage. This was done manually by making a 4–5 cm hole at an angle of 45° in the stalk with a needle bearing wooden handle and then toothpicks were inserted into the hole.

2.6. Disease scoring

Disease symptoms were scored at harvesting by splitting the stalk of inoculated plants. Longitudinally split stalks were individually scored on a 1–9 scale (Payak and Sharma, 1983), where a score of 1 = 25% discolouration of the inoculated node; 2 = 26–50% of the inoculated node; 3 = 51–75% of the inoculated node; 4 = 76–100% of the inoculated node; 5 = discolouration of the adjacent node, lesser than 50%; 6 = discolouration of more than 50% of the adjacent node; 7 = discolouration of more than three nodes; 8 = discolouration of more than four nodes; and 9 = discolouration of five nodes or broken or lodged plant due to disease. Disease score 1–2 was rated as highly resistant (HR), 2.1–4 as resistant (R), 4.1–6 as moderately resistant (MR) and > 6.1 as susceptible (S). In each row, at least 10 plants were inoculated and each inoculated plant was scored to obtain a mean disease score for the plot.

2.7. Statistical analysis

FSR and MSR scores data in different line evaluation trials were analysed using REML as implemented in CIMMYT Fieldbook (Bindiganavile et al., 2007). Variance components were estimated using Genstat (14th edition) (Payne et al., 2011). In hybrid trials, Griffing's Method 4 (no reciprocals, no parents) (Griffing, 1956) was used to compute the estimates of GCA and SCA. Analysis of variance (ANOVA) of hybrid trials was performed using PROC MIXED model in SAS version 9.4 (SAS, 2015) considering location, hybrids, replication as fixed effects and nested within location, and blocks as random effects and which are nested with in replication and location. Individual location variances were modelled into combined analysis. F-test was used for testing the significance of fixed effect factor and Z-test was used for testing the significance of random effect factor. The linear model for combined analysis of hybrids across locations for FSR and MSR were:

$$Y_{ijkl} = \mu + rep(loc)_{kj} + block(rep\ loc)_{jkl} + GCA_i + SCA_{ii'} + (GCA \times loc_{ij}) + (SCA \times loc_{ii'j}) + \epsilon_{ijkl}$$

In which, μ is the overall mean, $rep(loc)_{kj}$ is the effect of *k* replication within *j* location, $block(rep\ loc)_{jkl}$ is random effect of the *ith* incomplete block within *kth* replication and j location and is ~ NID(0, σ2b), GCA_i is ith parent general combining ability, i = 1 to p-1, $SCA_{ii'}$ is ii'^{th} hybrid specific combining ability, i' = i+1 to p, GCA × loc_{ij} is the interaction of GCA and location, SCA × $loc_{ii'j}$ is the interaction of SCA and location, and ϵ_{ijkl} is the random error ~ NID(0, σ2e).

The relative importance of GCA and SCA effects on inheritance of stalk rot resistance was assessed using the formula [$2MS_{GCA}$/($2MS_{GCA}$ + MS_{SCA})] (Baker, 1978; Lu and Myers, 2011). The closer the ratio is to unity, greater is the predictability of a specific hybrid's performance based on the GCA alone (Hung and Holland, 2012).

3. Results

3.1. Performance of inbred lines under artificial inoculation with FSR and MSR pathogens

LET 1 inbred trial for FSR at MPUAT and ICRISAT showed significant differences ($p < 0.01$) across locations, and hence single location analysis was done for this trial (Table 1). At both the locations, the genotypic variance was highly significant ($p < 0.01$), and hence the inbred lines were significantly different for FSR reaction from each other. The trial mean of disease scores of LET 1 at Hyderabad was 3.2,

Table 1
Analysis of Variance for line evaluation trials conducted under artificial inoculation at different locations for FSR (*Fusarium moniliforme*) and MSR (*Macrophomina phaseolina*).

	LET-1 (FSR)		LET-2 (FSR)		LET-3 (FSR)		LET-4 (MSR)	
Source of variation	DF	MS	DF	MS	DF	MS	DF	MS
Entry	84	4.9**	91	3.7*	109	0.80**	104	1.03*
Location	1	186.7**	_	_	_	_	1	897.45**
Entry.Location	84	2.9**	_	_	_	_	104	0.98*
Residual	164	1.3	92	2	105	0.5	201	0.72
Total	333		183		215		410	

Statistical Significance * $p < 0.05$, **$p < 0.01$, DF- Degree of freedom, MS – Mean sum of square.

Table 2
Response of CIMMYT Asia tropical maize germplasm to FSR and MSR *under* artificial inoculation at different locations during the year 2011 -2012.

Disease score	Hyderabad/LET 1	Udaipur/LET 1	Udaipur/LET 2	Hyderabad/LET 3	ICRISAT/LET 4	PJTSAU/LET 4
	FSR				MSR	
0-2.0	13	2	2	0	0	6
2.1-4.0	56	27	45	11	1	94
4.1-6.0	16	33	32	93	76	5
6.1-8.0	0	19	11	6	27	0
8.1-9	0	4	2	0	1	0
Mean	**3.2**	**5.0**	**4.4**	**4.9**	**5.5**	**3.0**
p	**	**	**	**	**	*
Min	**1.6**	**1.9**	**0.9**	**3.6**	**4.1**	**1.6**
Max	**5.6**	**9.0**	**8.3**	**6.8**	**8.4**	**4.8**
Heritability	**0.7**	**0.6**	**0.5**	**0.2**	**0.5**	**0.2**

Statistical Significance *p < 0.05, **p < 0.01, FSR- Fusarium stalk rot, MSR-Macrophomina stalk rot.

Table 3
Analysis of variance of F_1s developed from Diallel-A and Diallel-B for FSR evaluated at Hyderabad and MSR evaluated at Hyderabad and Ludhiana during the year 2013.

Source	FSR-Hyderabad				MSR across locations		MSR-Hyderabad		MSR-Ludhiana	
	Diallel-A		Diallel-B		Diallel -B					
	DF	F Value	DF	F Value	DF	F Value	DF	F Value	DF	F Value
ENV	_	_	_	_	1	27.07**	_	_	_	_
REP(ENV)	_	_	_	_	2	2.16	_	_	_	_
HYBRID	35	4.05*	65	1.96*	65	3.49**	65	1.95*	65	2.81**
GCA	8	23.4**	11	4.29**	11	11.17**	11	5.91**	11	6.89**
SCA	27	12.1	54	1.54	54	1.92**	54	1.11	54	1.79*
ENV*HYBRID	_	_	_	_	65	1.48*	_	_	_	_
GCA*ENV	_	_	_	_	11	2.61**	_	_	_	_
SCA*ENV	_	_	_	_	54	1.19	_	_	_	_
Estimates of random effects (Z- value)										
BLOCK(ENV*REP)		1.2		0.97		1.03		0.57		1.08
Residual-ENV 1 (Hyderabad)		0.26**		4.14**		4.35**		4.03**		3.88**
Residual-ENV 2 (Ludhiana)		_		_		4.51**		_	_	_
Predictability ratio (Baker ratio)		0.8		0.81		0.87		_	_	_

Statistical Significance * p < 0.05, ** p < 0.01, DF- Degree of freedom.

with minimum and maximum scores of 1.6 and 5.6, respectively and the broad sense heritability (H^2) estimate for the trial was 0.70 (Table 2). At Udaipur, inbred trials LET 1 and LET 2 showed trial mean disease scores of 5.0 and 4.4, and disease scores ranged from 1.9 to 9.0 and 0.9 to 8.3, respectively. The H^2 estimates of LET 1 and LET 2 were 0.5 and 0.6, respectively (Table 2) at Udaipur. LET 3 inbred trial conducted at ICRISAT, Hyderabad, showed a mean disease score of 4.9 with a disease score range of 3.9–6.8 and estimated H^2 of 0.20 (Table 2). Inbred lines VL1017256, VL1018129, VL107730, and VL0511321 had low FSR scores when screened under different trials. However, inbred lines VL1018172 and SNL142663 (supp. Table 3) consistently showed high FSR scores.

Analysis of inbred trial LET 4 conducted at ICRISAT and PJSTAU research farms for MSR revealed that the location × entry interaction was significantly different ($p < 0.05$); therefore, single site analysis was also done for this trial (Table 1). Inbred lines showed significant differences ($p < 0.01$ at ICRISAT; $p < 0.05$ at PJSTAU) in both the locations. The mean disease score of the trial at the ICRISAT farm was 5.5, with MSR scores ranging from 4.0 to 8.4. None of the genotypes were highly resistant to MSR. However, one genotype showed resistance reaction, 76 lines were moderately resistant, 27 lines showed susceptibility and one line was highly susceptible. The mean disease score of the LET 4 trial at the PJTSAU farm was 3.0, with a score ranging from 1.6 to 4.8. Six genotypes were found to be highly resistant, 94 were resistant and 5 were moderately resistant. None of the genotypes showed susceptibility to MSR at PJTSAU campus. The H^2 estimates of LET 4 were 0.2 and 0.5 at PJTSAU and ICRISAT, respectively (Table 2).

Inbred lines VL126, VL107730 and VL0511321 showed the lowest disease score, while SNL142663, VL1018172, and VL1018142 with the highest disease scores were used as susceptible parents to develop the diallel crosses for inheritance studies (Supp. Table 3).

3.2. General and specific combining abilities for FSR

Analysis of variance of hybrids developed from 9 × 9 (Diallel-A) and 12 × 12 (Diallel-B) partial diallels was studied for FSR. Variation among hybrids was significant ($p < 0.05$) in the hybrid trial for both Diallel-A and Diallel-B. GCA was significant ($p < 0.01$) in both the hybrid trials at the Hyderabad location, whereas SCA was found to be non-significant (Table 3). The heritability (repeatability) estimates of the trials conducted at the BISA farm, Ludhiana were close to zero, as the phenotypic variance was mostly due to error variance and none due to genotypic variance. Due to this, the data was not used for further analysis in order to avoid spurious results.

GCA effects of the genotypes used as resistant parents in Diallel-A showed negative and significant values, except inbred line, VL1249 which showed negative but non-significant GCA effects. Two inbred lines, VL1018159 and VL1018142 used as resistant lines in crosses showed positive but non-significant GCA effects (0.22 and 0.09, respectively). The highest negative and highly significant GCA effect was observed in VL1017256 (-0.61, $p < 0.01$) followed by VL108750 (-0.34, $p < 0.05$), both used as resistant parents. The highest positive and highly significant GCA effect was observed in SNL142662 (0.67, $p < 0.01$) followed by SNL142663 (0.36, $p < 0.05$), which were used as susceptible parents (Table 4). In Diallel-B, genotype VL107730 had

Table 4
Estimate of GCA effects for FSR of the parental lines used in 9 × 9 half Diallel-A evaluated at Hyderabad during the rainy season of 2013.

Sr. No.	Code	Pedigree	GCA effects
1	VL108750	CA00360/Pio3011F2-3-5-6-1	−0.34*
2	VL1018129	DTPWC9-F104-5-1-3-2-1-2-1	−0.31*
3	VL1017256	P390amC3/285 × 287F73-3-2-3 × MIRTC5AmF96-1-1-1-3-1)-1-1	−0.61**
4	VL1249	WLS-F299-2-1-2-B-2	−0.17
5	SNL142662	DTPYC9-F102-3-1-2-2-1-2-2-BB-B1	0.67**
6	SNL142663	CML311-2-1-1	0.36*
7	VL1018159	POOL16BNSEQC3F10 × 1-1-1-2-1	0.22
8	VL1018142	POOL16BNSEQC3F26 × 29-1-1-2-1	0.09
9	VL1018172	POOL16BNSEQC3F28 × 15-3-1-2-2	0.08

Statistical Significance * $p < 0.05$, **$p < 0.001$.

the highest negative and highly significant GCA effects (−0.58, $p < 0.05$) followed by inbred line VL109080 (−0.35, $p < 0.05$), indicating that these lines were the best combiners for FSR resistance in this set of parental lines (Table 5). Positive and highly significant GCA effects (0.85, $p < 0.01$) were observed in SNL142662 followed by VL1213 (0.53, $p < 0.01$). Negative but non-significant GCA effects were observed in resistant inbreds VL0511321 (−0.23), VL12180 (−0.34), VL109080 (−0.34), VL1018142 (−0.18) and VL1018172 (−0.13) (Table 4). Inbred SNL142662 showed highest positive and significant GCA effects ($p < 0.01$) in both Diallel-A and Diallel-B, thereby contributing to susceptibility to FSR (Tables 4 and 5).

The best five hybrids with the lowest disease scores for FSR in Diallel-A showed negative SCA effects, while the hybrids with highest disease scores showed positive values, except hybrid SNL14262 × VL1018142 (−0.03) which showed negative but non-significant SCA effect (Table 6). Of the best five hybrids, three showed the involvement of inbred line VL1017256 as one parent. Hybrid VL108750 × SNL142663 showed highest negative and significant SCA effects (−0.71, $p < 0.05$), followed by VL1017256 × VL1018172 (−0.45), while hybrid SNL142663 × VL1018159 showed highest positive and significant (0.87, $p < 0.05$) value. In Diallel-B, hybrid SNL142789 × VL1018142 showed the highest negative and significant SCA effect (−1.71, $p < 0.05$), followed by VL126 × VL107730 (−0.78). Hybrid VL126 × SNL142789 showed the highest positive and highly significant SCA effect (1.45, $p < 0.01$). It was observed that inbred line VL107730 was involved in three out of five most resistant hybrids (Table 6). The Baker ratio, which shows the relative importance of GCA over SCA, for Diallel-A and Diallel-B were 0.80 and 0.81, respectively (Table 3).

3.3. General and specific combining abilities for MSR

Sixty six hybrids developed from 12 × 12 half diallel crosses (Diallel-B) were used to analyse variance for MSR resistance in hybrids at two locations, Hyderabad and Ludhiana. The ANOVA showed highly significant variation due to environment, hybrid, GCA and SCA ($p < 0.01$). The interaction between hybrids × environment was significant ($p < 0.05$) and GCA × environment was highly significant ($p < 0.01$). However, there was no significant variation due to SCA × environment interaction (Table 3).

The inbred line VL107730 showed the largest negative and highly significant ($p < 0.01$) GCA effect at both Hyderabad and Ludhiana, respectively (−1.25 and −1.23) for MSR, followed by resistant line VL109080, which also showed negative (−0.70 and −1.20) and significant GCA effect ($p < 0.05$ and at Hyderabad and $p < 0.01$) at Hyderabad and Ludhiana, respectively. Resistant inbred line VL0511321 showed negative GCA effect (−0.34 and −0.84 at Hyderabad and Ludhiana, respectively) but was significant ($p < 0.05$) only at Ludhiana (Table 5). VL1018172 (GCA effect of 0.71 and 1.48 at Hyderabad and Ludhiana respectively) and SNL142662 (GCA effect of 0.49, 1.28 at Hyderabad and Ludhiana respectively) showed highest positive and significant GCA effects ($p < 0.01$) at both locations, indicating their contribution to susceptibility in a range of hybrids.

Highest negative and significant SCA effects were observed in hybrid VL107730 × SNL142663 (−1.77, $p < 0.05$), followed by VL107730 × VL0511321 (−1.04) at the Hyderabad location (Table 7). At Ludhiana, hybrid VL107730 × VL12180 showed highest negative and significant SCA effects (−2.49, $p < 0.05$) followed by hybrid VL126 × VL109080 (−1.86) (Table 7). Inbred lines VL107730 and VL0511321 were involved in lowest scoring hybrids for MSR at both the locations. The Baker ratio for MSR was 0.87, suggesting that additive gene effects are important for inheritance of resistance to MSR (Table 3).

4. Discussion

Developing resistant germplasm is one of the most economical and ecologically efficient strategies to manage stalk rots in maize. Among the different PFSR occurring worldwide, FSR, MSR and late wilt are more prevalent and destructive in the Asian tropics (Khokhar et al., 2014). FSR and MSR which are components of the PFSR complex of maize are serious biotic stresses in China, India, Indonesia, Pakistan, Philippines, Thailand and Vietnam. Hence, it is important to develop maize hybrids and varieties that are resistant to this disease, and thus be able to protect the true yield potential of these varieties when grown in agro-climates that favour the occurrence of these diseases. Therefore, this study evaluated CIMMYT Asia's lowland tropical maize germplasm under artificial inoculation at FSR and MSR hotspots, wherever possible, to identify resistant lines. Selected lines from line evaluation trials were used in specific mating designs to study the predominant gene action leading to resistance, and to study the combining abilities of these lines. The resistant lines identified, along with the combining

Table 5
Estimate of GCA effects for FSR and MSR of the parental lines used in Diallel-B evaluated at Hyderabad and Ludhiana during the dry and rainy season of the year 2013.

Sr No.	Names	Pedigree	FSR-Hyderabad	MSR-Hyderabad	MSR-Ludhiana
1	VL126	(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F191-1-1-1-B1	0.13	0.22	−0.24
2	VL107730	(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F203-1-1-1	−0.58*	−1.25**	−1.23**
3	VL0511321	[TS6C1F238-1-3-3-1-2-#-BB/[EV7992#/EV8449-SR]C1F2-334-1(OSU8i)-10-7(I)-X-X-X-2-BB-1]-1-1-2-1-1-B*5-1-B-B2	−0.23	−0.34	−0.84*
4	VL12180	CL-RCY031 = (CL-02410*CML287)-B-9-1-1-2	−0.34	−0.44	−0.0008
5	VL1213	(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F303-1-1-1	0.53**	0.27	−0.14
6	VL109080	G18SeqC5F19-1-2-1-2-2	-0.34	−0.70*	−1.20**
7	SNL142789	(DT/LN/EM-46-3-1xCML311-2-1-3)-B-F350-1-1-1	0.10	0.53*	−0.02
8	SNL142663	CML311-2-1-1	0.16	0.20	1.07*
9	SNL142662	DTPYC9-F102-3-1-2-2-1-2-2	0.85**	0.49*	1.28**
10	VL1018159	POOL16BNSEQC3F10x1-1-1-2-1	0.02	−0.13	0.49
11	VL1018142	POOL16BNSEQC3F26x29-1-1-2-1-BBB	−0.18	0.42	−0.66
12	VL1018172	POOL16BNSEQC3F28x15-3-1-2-2-BBB	−0.13	0.71**	1.48**

Statistical Significance *$p < 0.05$, **$p < 0.01$.

Table 6
Least square mean and SCA effects of highest and least FSR scoring hybrids of Diallel-A and Diallel-B at Hyderabad.

Diallel-A			Diallel-B		
Hybrids	FSR Score (1–9)	SCA Effects	Hybrids	FSR Score (1–9)	SCA Effects
VL1017256 × VL1018172	3.95	−0.45	SNL142789 × VL1018142	2.77	−1.71*
VL1017256 × VL1249	4.04	−0.1	VL107730 × VL0511321	3.19	−0.55
VL1017256 × SNL142663	4.18	−0.5	VL107730 × VL1018172	3.26	−0.58
VL108750 × SNL142663	4.24	−0.71*	VL126 × VL107730	3.33	−0.78
VL108750 × VL1249	4.27	−0.14	VL0511321 × VL12180	3.33	−0.66
SNL142663 × VL1018142	5.67	0.28	VL0511321 × SNL142662	6.1	0.91
VL1249 × SNL142662	5.8	0.35	VL126 × SNL142662	6.2	0.64
SNL142662 × SNL142663	6.08	0.07	VL1213 × SNL142662	6.2	0.3
SNL142663 × VL1018159	6.39	0.87*	VL126 × SNL142789	6.2	1.45**
SNL142662 × VL1018142	6.49	−0.03	SNL142789 × SNL142662	6.4	0.94
Mean	**4.95**			**4.55**	
Heritability	**0.69**			**0.61**	

Statistical Significance * $p < 0.05$, **$p < 0.01$.

abilities estimated in this study will serve two purposes: i) they will help to identify resistant lines to be used as resistant sources in population improvement, which could sometimes serve directly as improved open pollinated varieties with resistance to stalk rots in resource-poor regions in Asia, apart from being sources for deriving improved inbred lines; ii) Stalk rot resistant lines with high GCA and SCA effects could be used in hybrid breeding. Previous reports suggest that the genetics of different stalk rots in maize have been studied in different ecologies and germplasm in the context of the prevalent stalk rot pathogen causing PFSR world-wide (Santiago et al., 2010; Donahue et al., 1989; Callaway et al., 1990; Carson and Hooker, 1981; Khan and Paliwal, 1980).

4.1. Inbred line evaluation for FSR and MSR

Three inbred line evaluation trials (LET 1, LET 2 and LET 3) for FSR were conducted under artificial inoculation at two locations of Udaipur and Hyderabad during 2011 and 2012. Inbred lines exhibited significant differences for FSR incidence at both the locations and years. Greater FSR severity was observed at Udaipur compared to Hyderabad, which could have been because Udaipur is a hotspot location for FSR. Environmental conditions like warmer temperature, lower rainfall and soil fertility is known to assist in natural root infection of the FSR pathogen, and hence this location is considered as a hotspot location for this disease. Despite the differences in disease severity across the two locations, inbred lines VL0511321, VL108750, VL1018129 and VL1017256 showed consistently low FSR scores and could therefore be used as environmentally stable resistant sources for FSR in population improvement programs. The test cross performance for grain yield of these inbred lines in combination with the tester lines were also found to be good; VL0511321 showed grain yield of 6.22 tons per hectare when crossed with CIMMYT B- group tester CML470. Similarly, inbred lines VL108750, VL1018129 and VL1017256 showed grain yields of 5.06, 6.45, and 5.84 tons per hectare, respectively in test crosses with CIMMYT testers (data not shown).

Inbred lines were also evaluated for MSR, typically characterized by black charcoal like lesions inside the stalk. Line evaluation trial LET 4 screened for MSR at ICRISAT showed more susceptibility reaction than the LET4 trial at PJTSAU. The LET 4 trial at ICRISAT was exposed to mild drought at flowering stage, which could have resulted in higher disease incidence in the trial. This was observed by Edmunds (1964) and Odvody and Dunkle (1979) that subjecting plants to water stress after inoculation and during reproductive stage may lead to latent infections develop scorable lesions. Inbred lines VL0511321, VL126 and VL107730 showed low MSR scores at both the locations and hence could be considered as stable resistant sources of MSR. The test cross performance of these lines for grain yield were 6.22, 4.43 and 5.75 tons per hectare in test crosses with elite CIMMYT testers (Data not shown).

4.2. Gene action and combining abilities for FSR

Two partial diallels were formed to study the gene action and estimate GCA and SCA, which are in turn important considerations in further resistance breeding. Diallel mating design IV was employed, which helps to overcome the competition effects between pure inbred line parents and F_1s (Hallauer. et al., 2010), as only diallels without reciprocals are evaluated in trials excluding parents. Hybrid trials were evaluated at two locations for FSR, Hyderabad and Ludhiana. The repeatability of the trials in Ludhiana was close to zero, where most of the

Table 7
Least square mean and SCA effects with scoring highest and lowest MSR scoring hybrids of Diallel-B at Hyderabad and Ludhiana.

Hyderabad			Ludhiana		
Hybrids	MSR Score (0-9)	SCA Effects	Hybrids	MSR Score (0-9)	SCA Effects
VL107730 x VL0511321	2.7	-1.04	VL107730 x VL0511321	2.96	−1.07
VL12180 x SNL142663	3.4	-0.94	VL107730 x VL12180	3.05	−2.49*
VL107730 x SNL142663	3.4	-1.77*	VL126 x VL109080	3.15	−1.86
VL126 x VL107730	3.55	-0.81	VL107730 x VL109080	3.3	−1.61
VL12180 x VL109080	3.75	-0.5	VL0511321 x VL1213	3.4	−1.03
SNL142789 x SNL142662	7.05	1.4	SNL14266 x SNL142662	8.95	−0.04
VL12180 x VL1018172	7.05	0.59	VL1018159 x VL1018172	9	1.11
SNL142789 x SNL142663	7.1	0.87	VL12180 x VL1018172	9	0.98
SNL142662 x VL1018142	7.1	0.7	SNL142662 x VL1018172	9.15	−0.07
VL1018142 x VL1018172	7.3	0.64	VL126 x SNL142663	9.45	2.21*
Mean	**5.44**			**6.33**	
Heritability	**0.53**			**0.65**	

Statistical Significance * $p < 0.05$, ** $p < 0.01$.

phenotypic variance observed was due to the error variance and not from the genotypic variance. Hence the hybrid trial conducted at Ludhiana was not used for further analyses and inferences. Analysis of variance for FSR in Diallel-A and Diallel-B, hybrids were found to be significantly different at Hyderabad location. Among the combining ability components, GCA was found to be significantly different in both the diallels, which indicated high variability of GCA among the parents, and suggests that genetic gain is achievable to improve FSR resistance through selection (Arunga et al., 2010). SCA variance was found to be non-significant, suggesting the preponderance of additive gene action for FSR resistance at this location. It suggests that early generation testing would be effective and selection of hybrids could be solely based on the prediction of GCA effects (Badu-Apraku et al., 2015). The relative importance of GCA and SCA effects was estimated by the ratio of GCA effects to the total genetic effect (Baker, 1978). The closer the ratio is to unity, suggests that hybrid performance can be accurately predicted based on the average of parental GCA values. Significant GCA and a higher Baker ratio indicated that inheritance of FSR resistance of the hybrids studied were governed by additive gene action. Our results were in accordance with Donahue et al. (1989), who reported that estimates of GCA and SCA effects were significant, with a predominance of GCA effects, for stalk rots caused by *Diplodia maydis* and *Fusarium moniliforme*. Similarly, results from Santiago et al. (2010) suggested that GCA and SCA effects of Gibberella stalk rot caused by *Fusarium graminearum* were significant and the GCA/SCA ratio was higher showing that additive gene action was controlling Gibberella stalk rot resistance in maize. Studies done by Lunsford et al. (1974, 1976) revealed that additive gene action and maternal effects are more important than dominant gene action in the inheritance of resistance to seedling blight of maize caused by *Fusarium moniliforme.* Since reciprocal crosses were not studied, we were not able to make any inference regarding maternal effects towards resistance to FSR.

Inbred lines VL1087256 and VL107730 showed highest negative GCA effects for FSR resistance in Diallel-A and Diallel-B, respectively indicating that they could contribute favourable alleles in a range of breeding crosses to develop FSR-resistant hybrids. Makumbi et al. (2011) and Badu-Apraku and Oyekunl, (2012) suggested that such inbred lines could be used to develop synthetic populations that could be improved for stress environments. In this study, inbred lines having highest negative GCA effects developed highly resistant hybrids VL1017256 × VL1249 and VL108750 × VL1249 in Diallel-A and VL107730 × VL0511321 and VL107730 × VL1018172 in Diallel-B. Similarly, inbred lines with positive GCA effect estimates developed hybrids with high disease scores in both diallel experiments (Tables 4 and 5). Some hybrids (VL1017256 × VL1018172 and SNL142789 × VL1018142) showed high resistance when one inbred line with negative GCA effect for FSR was crossed with another inbred line having positive GCA effect, in which case, dominant or epistatic gene action cannot be ruled out.

4.3. Gene action and combining abilities for MSR

One partial 12 × 12 diallel (Diallel-B) in Diallel mating design IV was formed to study the gene action and combining abilities for MSR in CIMMYT's tropical maize germplasm. The hybrid combinations were evaluated at Hyderabad and Ludhiana locations. The interaction between hybrids × environment and GCA × environment were significant, suggesting that for development of hybrids resistant to MSR, it is important to select specific parental lines for specific environments. High significance of GCA and SCA variance revealed that additive and non-additive gene actions were important for MSR resistance. The high Baker ratio indicated that additive gene action is more important than non-additive gene action to impart resistance to MSR. Similar observation that additive gene effects were predominant over non-additive effects for charcoal rot (MSR) resistance in maize was reported by Singh and Kaiser (1991). Inheritance study of *F. moniliforme* and *M. phaseolina* by Bramelcox et al. (1988) in sorghum concluded that resistance to both the organisms depends on several to many loci. Resistance could be dominant at some loci in some parents but recessive in others. They also concluded that GCA is important to both the diseases, and especially MSR in sorghum. However, results from our study contradict Krishna et al. (2013) who reported that the magnitude of dominance was higher than additive effects, suggesting that charcoal rot resistance in maize was governed by dominance effect, even though his study also observed additive effect. The predominance of additive gene effects observed in this study suggests that the best progeny might be derived from crosses with genotypes having highest negative GCA. Our experimental results also suggest that inbred line VL107730 having the highest negative and highly significant GCA effect (−1.25 and −1.23 at Hyderabad and Ludhiana, respectively) developed resistant hybrids when crossed with other inbreds having negative GCA effects like, VL107730 × VL0511321 and VL107730 × VL12180 (Table 7) suggesting the additive gene action for MSR resistance. Hybrid VL107730 × VL0511321 showed the least MSR score at both the locations. Inbred line VL107730 was found to be a good combiner for both FSR and MSR.

4.4. Breeding for stalk rot resistance in tropical maize

Considering the importance of stalk rots as a major bottleneck in the tropics for attaining the maximum yield potential in maize, incorporating resistance to these diseases is considered as a major breeding objective in tropical maize breeding. Population improvement to develop open pollinated varieties or for development of superior inbred lines for hybrid combinations is one of the major activities towards this. As our experimental results indicated preponderance of additive gene action for both FSR and MSR, population improvement through recurrent selection either through S_1 progeny selection or through bi-parental full-sib family selection could be used to develop stalk rot resistant populations (Khan and Paliwal, 1980). Recurrent selection schemes exploit additive, partial dominance to dominance and over dominance types of gene actions. Recurrent selection for GCA is more effective than other schemes when additive gene effects are more important. Recurrent selection procedures were used by Jinahyon and Russell (1969) to develop resistance to stalk rot caused by *Diplodia zea* in open-pollinated variety Lancaster surecrop, which had high susceptibility to stalk rot. Recombination of superior progenies increase the frequency of favourable alleles, which in future cycles increase the opportunities of deriving better progenies with desired standards of most traits (Hallauer. et al., 2010). Hallauer (1973) suggested that three to four cycles of recurrent selections seem sufficient to develop populations that have acceptable levels of resistance. Genetic improvement using S_1 or S_2 families has been used for a broad range of traits (Hallauer, 1992; Oyervides-Garcia and Hallauer, 1986), when additive gene effects are predominant. According to Hallauer. et al. (2010), the S_1 or S_2 selection on the progeny and evaluation of S_1 or S_2 testcross could be used to select the progenies with superior GCA and SCA. S_1 or S_2 testing done in this manner is useful in identifying superior inbred lines that can be recurrently selected to develop better inbred lines. The lines that were found to have high resistance and high GCA effects could be directly used in a range of hybrid combinations for appropriate ecologies, considering the significant GCA × environment effects observed for MSR resistance. Similarly, specific cross combinations with high SCA could be used directly as hybrid varieties, after testing for superior yields. Based on this study, the best hybrids have already been selected from the two diallels, and recurrent selection schemes have been initiated for population improvement and improved inbred line development with resistance to stalk rots.

Author contribution statement

Designed the experiments: SN, PHZ; Conducted the experiments: ZR, PS, MTV, SSS, MKK; Analysed the data: ZR, AK, AR; Wrote the

manuscript: SN, ZR, AK.

Conflicts of interest

The authors declare that they have no conflict of interest.

Ethical standards

The authors declare no ethical standards have been violated in the course of the study.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cropro.2017.12.004.

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