Received: 25 August 2016 | Accepted: 22 April 2017

DOI: 10.1111/pbr.12492

ORIGINAL ARTICLE

WILEY Plant Breeding

Genetic analysis of mechanisms associated with inheritance of resistance to sheath rot of rice

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Funding information
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Communicated by Z.-K. Li

Abstract

Understanding genetic mechanisms controlling inheritance of disease resistance traits is essential in breeding investigations targeting development of resistant genotypes. Using North Carolina design II, 32 F_1 hybrids were generated by crossing eight susceptible to four resistant parents and submitted for field evaluation. The analysis of general and specific combining ability (GCA and SCA) indicated involvement of additive and non-additive gene action controlling inheritance of horizontal resistance to sheath rot of rice. High GCA/SCA ratio and high heritability estimates revealed additive effects and were more predominant than none additive ones. The level of dominance indicated dominant genes was more important than recessive genes. Estimates of GCA and SCA analysis suggested that crop improvement programmes should be directed towards selection of superior parents or good combiners, emphasizing on GCA. As far as source of resistance is concerned, most promising genotypes were Cyicaro, Yunertian and Yunkeng. The predominance of additive genetic effects together with the relevance of dominant genes suggested possibilities of improving the resistance by introgression of resistance genes through recurrent selection coupled with phenotypic selection.

KEYWORDS
additive effects, combining ability, gene action, resistance breeding, sheath rot of rice

1 | INTRODUCTION

Rice production frequently faces constraints due to both biotic and abiotic stresses and among others; the sheath rot (ShR) caused by *Sarocladium oryzae* [(Sawada) W. Gams & D. Hawksworth]. The disease has become endemic in almost all the rice growing regions around the world in both rainfed and irrigated ecosystems and is now considered as one of most important emerging and destructive disease of rice (Hittalmani, Mahesh, Mahadevaiah, & Prasannakumar, 2016; Madhav et al., 2013).

The disease affects all types of rice varieties with high incidences reported in modern cultivars (Miah, Shahjahan, Hossain, & Sharma, 1985). Dwarf and high yielding Asian varieties are more susceptible, whereas tall varieties with well-exerted panicles are resistant. ShR of rice damages the uppermost flag leaf sheath covering the young panicles. Under severe conditions, panicles fail to fully emerge and remain enclosed in the flag leaf sheaths (Estrada, Sanchez, & Crill, 1979 and Naeimi, Okhovvat, Hedjaroude, & Khosravi, 2003). This leads to poor panicle formation, followed by increased number of chaffy, discoloured and shrivelled grains, thus reducing weight and number of healthy grains. Yield losses range between 20% and 30% in general, but severe losses up to 70%–85% were reported in several parts of the world (Pearce, Bridge, & Hawksworth, 2001 and Sakthivel, 2001).

Similar to diseases of rice, the deployment of varietal resistance has always been considered as the most economically and environmentally friendly approach. In breeding for resistance to endemic diseases, horizontal resistance is often preferred to vertical resistance (Vanderplank, 1984). This is because horizontal resistance operates

against all pathotypes and so there is no differential interaction between pathotypes and cultivars, whereas vertical resistance is oligogenic and race-specific and can be overcome by a change of race.

While Mulbah, Shimelis, and Laing (2015) and Vanderplank (1984) attested that components of horizontal resistance include traits such as lesion size, and speed at which lesion spreads over the affected leaf area. Srinivasachary, Shailaja Hittalmani, Girish Kumar, Shashidhar, and Vaishali (2002) and Vinod, Vivekanandan, and Subramanian (1990) reported a strong relationship between sheath rot of rice and panicle exsertion. However, because the disease has for long time been considered as minor, little information is available on its genetic variation, mode of gene action and nature of inheritance of resistance. According to Falconer, Mackay, and Frankham (1996) and Sprague and Tatum (1942), determination of combining ability is important not only for gene action determination, but also parental selection in hybridization programmes.

Therefore, this study was conducted to estimate the combining ability effects for resistance to sheath rot among selected rice lines and determine the gene action controlling sheath rot resistance.

2 | MATERIALS AND METHODS

2.1 | Plant materials

The crossing block of this study consisted of eight (female) and four (male) sheath rot susceptible and resistant varieties, respectively, all kindly availed by the Rice Research Programme of Rwanda Agriculture Board (RAB), generating hence 32 F_1 progeny. All these parental lines are given in Table 1.

Hybridization was performed following an 8 × 4 North Carolina Design II (NCDII) mating design, in the tunnels of RAB's Rubona station, during the season of September to December, 2014.

All the 32 crosses and their 12 parental lines were subjected to field evaluation in Rurambi; one of irrigated rice schemes in the Eastern Province of Rwanda. The location had been cultivated with rice for a long time as an intensive monoculture without rotation and ShR of rice was previously confirmed to be endemic in the area and hence a good disease hotspot with a mixture of physiological races and isolates.

However, the NCDII crosses did not generate enough F_1 seeds; hence, the F_1 plants were increased through clonal propagation by tiller transplanting method.

2.2 | Experimental layout and design

The experiment was laid out in an 11 × 4 alpha lattice design and replicated twice, between January and June 2015. Although the experimental site was a disease hot spot, plants were artificially inoculated to obtain uniform disease infection. In each experimental plot, five plants of 25 were randomly selected and tagged for artificial inoculation and various data collection measurements.

The crop was raised under aerobic condition by providing continuous irrigation. Except fungicide applications, the rest of the cultural practices and crop protection measures were applied as recommended, thus ensuring uniform and healthy crop growth.

TABLE 1 List of parental lines used and their reaction to ShR of rice

	Code	Name	Varietal reaction to ShR	Panicle exsertion
Males	P1	Cyicaro	Moderately resistant	Exserted
	P2	Nyiragikara	Highly resistant	Well exserted
	P3	Yunertian	Highly resistant	Well exserted
	P4	Yunkeng	Resistant	Well exserted
Females	P5	Buryohe	Highly susceptible	Partially exserted
	P6	Fac 56	Susceptible	Partially exserted
	P7	Fashingabo	Susceptible	Partially exserted
	P8	Gakire	Susceptible	Enclosed
	P9	Intsinzi	Highly susceptible	Enclosed
	P10	Mpembuke	Susceptible	Partially exserted
	P11	Ndamirabahinzi	Susceptible	Partially exserted
	P12	Rumbuka	Highly susceptible	Partially exserted

2.3 | Data collection and analysis

Data were collected on a fortnightly basis on ShR horizontal resistance-related traits, namely lesion size (LS) and panicle exsertion (PE), starting a few days after booting stage. LS was evaluated as lesion length (in cm). From the LS, the area under disease progress curve (AUDPC) was determined using the formula described by Simko and Piepho (2012).

PE was evaluated by metric measurement (cm) of the length of uppermost internode above the flag leaf sheath or panicle rachis.

Mean performance of each cross and parental line was determined through the analysis of variance using REML procedure of Genstat 17th edition (Payne, Welham, & Harding, 2014).

Genetic parameters were determined from the expected mean squares from the analysis of variance of the NCDII performed on F_1 progeny as described by Acquaah (2012) and given in Table 2 where variations are partitioned into differences between males (m), females (f) and their interaction.

In this variations in crosses were partitioned into general combining ability (GCA) and specific combining ability (SCA) following a genetic model as described by Simmonds (1979).

$$Y_{fmk} = \mu + GCA_f + GCA_m + SCA_{fm} + rk + e_{fmk},$$

where Y_{fmk} is the mean of the cross between female (f) and male (m) parents; GCA_f and GCA_m are general combining abilities for female and male parents respectively; SCA_{fm} is the specific combining ability

TABLE 2 Analysis of variance for NCD II and test of effects

Source of variation	Degree of freedom	Mean squares	*F* test
GCAf	f-1	MSf	MSf/MSf
GCAm	m-1	MSm	MSm/MSfm
SCAmf	(f-1)(m-1)	MSfm	MSfm/MSe
Error	Fm (r-1)	MSe	

between female f and male m; rk is the replication effects; e_{fmk} is the error term.

The GCA for each of the male and female parents was calculated using following formulas as described by Acquaah (2012):

$$GCA_m = X_m - \mu$$

$$GCA_f = X_f - \mu$$

The SCAs of the crosses were computed from the formula:

$$SCA_X = X_X - E(X_X) = X_X - [GCA_m + GCA_f + \mu],$$

where GCA_m = general combining ability of male parent; X_m = Mean of the male parent; μ = Overall mean of all crosses; GCA_f = general combining ability of the female parent, X_f = mean of the female; SCAX = specific combining ability of the two parents in the cross; X_X = observed mean value of the cross; $E(X_X)$ = expected values of the cross basing on the GCAs of the two parents.

Using mean square for GCA (MSg), SCA (MSs) and Error (MSe) extracted from the ANOVA table of the NCDII analysis, variance components, such as additive (σ^2A), non-additive (σ^2NA) and Environmental (σ^2E) variances, were deducted as follows, according to Acquaah (2012):

$$\sigma^2 f = \frac{[MSf - MSfm]}{rm} = \frac{1}{4}VA = \text{additive variance}$$

$$\sigma^2 m = \frac{[MSm - MSfm]}{rf} = \frac{1}{4}VA = \text{additive variance}$$

$$\sigma^2 mf = \frac{[MSfm - MSe]}{r} = \frac{1}{4}VNA = \text{non-additive variance}$$

where σ^2 = variance; MSm = mean square based on male parents; MSf = mean square based on female parents; m = number of males; f = number of females; and r = number of replications.

$$\sigma^2 e = MSe = \frac{1}{2}VA + \frac{3}{4}VNA + E = \text{environmental variance.}$$

Heritability in broad sense (H^2) and narrow sense (h^2) were estimated as follows:

$$H^2 = \frac{(\sigma^2 A + \sigma^2 NA)}{(\sigma^2 A + \sigma^2 NA + \sigma^2 E)}$$

$$h^2 = \frac{(\sigma^2 A)}{(\sigma^2 A + \sigma^2 NA + \sigma^2 E)}$$

Other parameters estimated include maternal effects, GSCA/SCA ratio and level of dominance.

3 | RESULTS

3.1 | Mean performance of crosses and parents

The analysis of variance using REML procedure revealed highly significant differences ($p < .001$) between all genotypes for LS, AUDPC and PE.

The mean value of each trait varied significantly with specific genotypes (Table 3).

The mean LS for parental lines and derived crosses ranged from 0.47 cm to 18.97 cm with female parents recording higher scores than male parents.

Mean LS for crosses ranged between 7.22 cm and 14.02 cm. Crosses involving P10 (Nyiragikara) as source of resistance recorded highest values of LS, whereas crosses which recorded least LS size were those involving P11 and P12 (Yunertian and Yunkeng), respectively.

Mean PE values for all the genotypes varied between 2.22 and 9.32 with evidently male parental lines, recording lowest values compared to female parents and crosses. Most well-exerted crosses were the ones involving P11 (Yunertian) and P10 (Nyiragikara), where the least values were obtained with crosses involving P12 (Yunkeng), P10 (Nyiragikara) and P9 (Cyicaro).

3.2 | Analysis of combining abilities

The analysis of NCDII (Table 4) revealed variances due to GCA for both male and female parents that are highly significant ($p < .01$) for LS, AUDPC and PE. Variances due to SCA were significant ($p < .05$) for, only, AUDPC and PE. On the other hand, GCAm/SCA ratio and GCAf/SCA ratios were greater than one for all the traits, but the highest ratio was obtained on PE. Maternal effects were not significant for all the traits.

In addition to GCA and SCA estimates, individual GCA and SCA and their effects, for both parental lines and crosses revealed considerable variations among different genotypes (Table 5, Figures 1 and 2).

From Table 5, Rumbuka recorded the highest positive GCA for AUDPC (34.68) and LS (2.67 cm) fundamentally for susceptibility, whereas the highest GCA effect for PE was recorded on Mpembuke (1.467 cm). In contrast, Intsinzi had the highest negative GCA for both AUDPC (−19.194) and LS (−1.47) whereas Fac 56 recorded least values of PE (−1.253).

SCA of crosses illustrated on Figures 1 and 2 indicated that highest positive effects were recorded on Cyicaro × Buryohe for AUDPC (27.231), Nyiragikara × Fac 56 (1.89) for LS and Nyiragikara × Fashingabo for PE (0.451). The highest negative effects were found on Nyiragikara × Gakire for AUDPC (−25.294) and LS (−1.64), and Cyicaro × Rumbuka for PE (−0.448).

Of 32 crosses, 18 were most genetically important as far as AUDPC and LS are concerned, as they recorded negative values of SCA.

These include crosses identified as P2XP9, P3XP9, P5XP9, P7XP9, P8XP9, P1XP10, P3XP10, P4XP10, P8XP10, P1XP11,

TABLE 3 Mean values for parental lines and crosses for LS and PE

Parental materials								
Females	**Buryohe**	**Fac 56**	**Fashingabo**	**Gakire**	**Intsinzi**	**Mpembuke**	**Ndamiraba-hinzi**	**Rumbuka**
LS (cm)	18.64	17.92	4.93	14.96	15.96	10.27	11.36	18.97
PE (cm)	4.73	2.22	5	5.21	4.59	8.16	7.18	4.82
Males	**Cyicaro**	**Nyiragikara**	**Yunertian**	**Yunkeng**				
LS (cm)	1.67	0.51	0.47	1.47				
PE (cm)	7.83	9.23	9.32	7.93				

Crosses									
		Females							
Males	**Trait**	**Buryohe**	**Fac 56**	**Fashingabo**	**Gakire**	**Intsinzi**	**Mpembuke**	**Ndamirabahinzi**	**Rumbuka**
Cyicaro	LS (cm)	13.21	12.27	11	9.92	9.44	13.6	8.47	9.57
	PE (cm)	5.22	5.48	6.43	5.84	4.54	4.52	5.14	4.47
Nyiragikara	LS (cm)	8.6	9.29	8.26	8.06	10.66	9.39	9.15	8.63
	PE (cm)	5.55	6.54	6.02	5.8	5.73	5.95	5.83	5.87
Yunertian	LS (cm)	8.44	9.89	8.73	7.31	9.53	12.28	9.3	9.09
	PE (cm)	5.17	5.79	6.17	5.14	7.23	7.07	8.08	7.2
Yunkeng	LS (cm)	8.09	11.57	7.22	9.4	12.33	14.02	11.96	12.44
	PE (cm)	6.16	7.09	6.79	6.41	4.78	5.7	6.47	5.5

P2XP11, P6XP11, P7XP11, P2XP1, 2P1XP12, P5XP12, P6XP12, P8XP12, for AUDPC (Figure 1) and P2XP9, P5XP9, P6XP9, P7XP9, P8XP9, P1XP10, P3XP10, P4XP10, P5XP10, P8XP10, P1XP11, P2XP11, P6XP11, P7XP11, P1XP12, P5XP12, P6XP12, P8XP12 for LS (Figure 2).

On the other hand, 16 crosses of 32 were genetically important as they recorded positive values of SCA as far as PE is considered (Figure 2).

These include P1XP9, P3XP9, P5XP9, P7XP9, P8XP9, P1XP10, P2XP10, P6XP10, P3XP11, P4XP11, P7XP11, P2XP12, 3XP12, 5XP12, P6XP12, P7XP12. A number of crosses showing high SCA effects involved parents with high × low or low × high GCA, low × low GCA or low × average GCA.

TABLE 4 Analysis of a 8 × 4 North Carolina Design II for combining ability estimates for LS, AUDPC and PE

Source of variation	LS	AUDPC	PE
GCAm	94.772**	16458.884**	9.122**
GCAf	58.329**	14865.770**	25.362**
SCA mf	9.669 ns	2266.817*	0.966*
Error	6.558	1286.791	0.597
GCAm: SCA ratio	9.802	7.261	9.443
GCAf: SCA ratio	6.0326	6.5580	26.2547
Maternal effects	1.625 ns	1.107 ns	0.360 ns

GCAm, general combining ability based on male parents; GCAf, general combining ability based on female parents; SCA, specific combining ability of crosses.
* and ** represent significant effects of GCA and SCA at 1% and 5%, respectively.

3.3 | Variance components and genetic parameters

The analysis of genetic effect on the mechanisms associated with inheritance to ShR of rice was estimated based on variance components as shown in Table 6. From this table, a large proportion of variation was due to parental lines rather than crosses based on low level of SCA variance and estimates of variation within full sibs. On the other hand, the additive component of genetic variation was greater than non-additive and environmental component of variation

TABLE 5 Estimates of GCA of parental lines for AUDPC, LS and PE

Genotype	Code	LS	AUDPC	PE
Buryohe	P1	1.58**	19.756 **	−0.178
Fac 56	P2	0.27	6.056	−1.253**
Fashingabo	P3	−1.49**	−18.394**	0.049
Gakire	P4	−0.62*	−10.044	−0.078
Intsinzi	P5	−1.47**	−19.194**	−0.361**
Mpembuke	P6	−0.01	0.031	1.467**
Ndamirabahinzi	P7	−0.94**	−12.894*	0.669**
Rumbuka	P8	2.67**	34.681**	−0.313*
Cyicaro	P9	0.08	−0.031	−0.345**
Nyiragikara	P10	1.47**	20.294**	0.094
Yunertian	P11	−0.71	−10.194**	0.428**
Yunkeng	P12	−0.84*	−10.069**	−0.177*

GCA estimates followed by * and ** are statistically significant at 1% and 5% levels of significance, respectively. GCA estimates showing highest positive and significant values indicate good combiner parents for some traits.

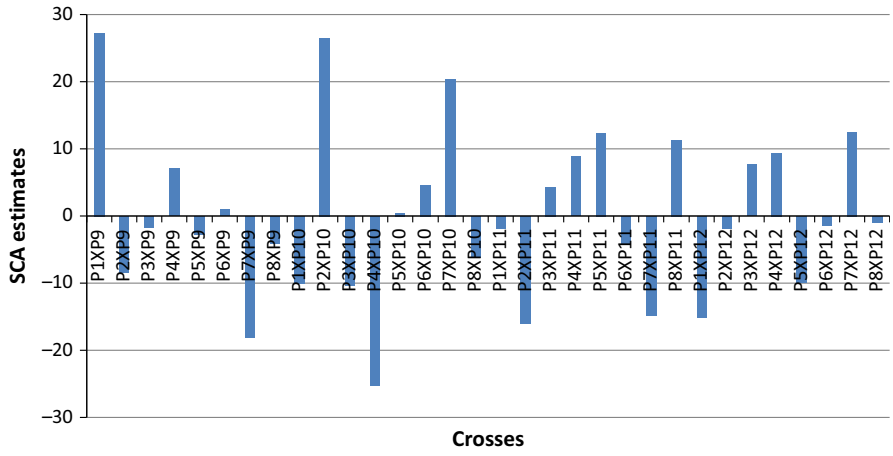

FIGURE 1 Specific combining ability for area under disease progress curve [Colour figure can be viewed at wileyonlinelibrary.com]

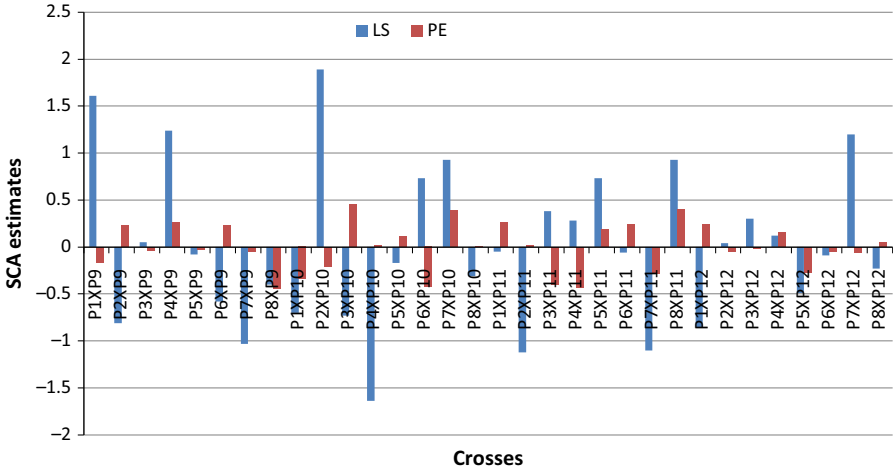

FIGURE 2 Specific combining ability for lesion size and panicle exsertion [Colour figure can be viewed at wileyonlinelibrary.com]

for all the studied traits. Variations within full sibs were greater than GCA and SCA only for lesion size. Following the same trend, additive variance either based on male and female parents was greater than non-additive variance.

Heritability in broad sense was higher than heritability in narrow sense. Broad sense heritability ranged between 66.6% and 89.2% for all the studied traits, whereas narrow sense heritability varied from 63.7% to 88.9%. PE recorded the highest heritability estimates, whereas LS showed lowest heritability. The analysis of level of dominance was between 0 and 1 for all the studied traits except PE.

4 | DISCUSSION

4.1 | Performance of parental lines and crosses

The analysis of variance revealed significant differences, at both 5% and 1%, for the three evaluated traits associated with horizontal resistance to ShR of rice, namely, LS, AUDPC and PE. These results proved the existence of considerable variability among parental materials and progeny that can be exploited for cultivar improvement.

This variability among genotypes might be due to genetic make-up of each of parental lines, which may have been evolved from different gene pools. This statement is in line with suggestions by Ngala and Adeniji (1986).

4.2 | Combining ability effects

In this study, both GCA and SCA revealed significant differences for the studied traits except SCA for lesion size. Male and female parents revealed considerable variability as far as GCA is concerned. Parental lines with highest and positive scores were considered bad combiners because positive effects for disease resistance-related traits indicate increased level of disease susceptibility. According to Bokmeyer, Bonos, and Meyer (2009), negative GCA and SCA effects are desirable for disease resistance, based on a scale where the highest value corresponds to more disease attack. In these regards, genotypes such as Ndamirabahinzi, Intsinzi, Fashingabo, Yunkeng, Cyicaro and Yunertian were identified as good combiners for LS and AUDPC as they recorded highest negative scores of GCA.

Some of the crosses showing high SCA effects involved parents with high × low GCA or low × high GCA, low × low GCA or low × average GCA. The high SCA effects of such crosses might be attributed to additive × additive type of gene action and the high disease resistance potential of these crosses can be fixed in subsequent generations (Chakraborty, Chakraborty, Dutta, & Paul, 2009). According to the same source, crosses generated from high general combiner parents exhibiting high negative SCA effects are expected to produce useful transgressive segregants, which can be identified following simple conventional breeding technique like pedigree method of selection.

TABLE 6 Variance components and related genetic parameters for LS, AUDPC and PE

Estimated parameter	LS	AUDPC	PE
Variation between females or GCAf variance (σ^2f)	5.319	887.004	0.510
Variation between males or GCAm variance (σ^2m)	6.083	1574.869	3.050
Variation due to interaction between males and females SCA variance (σ^2mf)	1.556	490.013	0.185
Variation within full sibs	6.558	1286.791	0.507
Additive variance of males (σ^2Af)	21.276	3548.017	2.039
Additive variance of females (σ^2Am)	24.330	6299.477	12.198
Non-additive variance (dominance or epistasis) (σ^2D)	6.222	1960.052	0.738
Environmental variance (σ^2e)	15.304	3244.047	1.573
Broad sense heritability based on females (H^2f)	0.666	0.718	0.892
Narrow sense heritability based on males (h^2m)	0.637	0.637	0.889
Level of dominance based on males (dm)[a]	0.332	0.035	1.192
Level of dominance based on females (df)	0.290	0.020	0.199

[a]Relevant only when maternal effects are significant.

Conversely, high SCA effects of the crosses that resulted from high × low combining parents are attributed to additive × dominance type of gene action (Sharma, Singh, Mall, Kumar, & Singh, 2014). The high level of resistance from such crosses would be unfixable in subsequent generations. Nevertheless, these crosses would produce desirable transgressive segregants in later generations by modifying the conventional breeding methodologies to capitalize on both additive and non-additive genetic effects (Chakraborty et al., 2009).

Brown, Caligari, and Campos (2014) reported that, when SCA is small to GCA, it is possible to predict the performance of a particular cross-combination based on the values of GCA of parents. Consequently, because GCA estimates were greater that SCA in this study, good combiner parents are useful for prediction of introgression of ShR resistance genes into progeny. As far as source of resistance is concerned, good combiners or potential male parental lines with significant negative GCA include Cyicaro, Nyiragikara and Yunkeng. Elsewhere, for a varietal improvement programme involving susceptible parents, best combiners should include, Fashingabo, Gakire, Intsinzi and Ndamirabahinzi, as they all have significant and highest negative GCA.

4.3 | Gene action

From the genetic point of view, GCA measures additive gene effects, whereas SCA is the expression of non-additive affects, either dominance or epistasis (Bradshaw, 2016).

In this study, GCA effects were highly significant for all the traits, whereas SCA was not significant only for LS. Therefore, both additive and non-additive gene effects were important in the mechanisms of expression of these traits associated with resistance to ShR. Non-significant SCA for LS suggests that non-additive effect of genes was less important. Reports by Reif, Gumpert, Fischer, and Melchinger (2007) suggest that in the absence of epistasis, GCA seems predominant over SCA and the relevance of dominance effects tends to decrease. In these regards, the ratios of GCA/SCA were all greater than one, suggesting additive effects were most predominant than non-additive ones.

The involvement of mostly additive gene effects in the mechanism of resistance to ShR was also reported by Srinivasachary et al. (2002). With the predominance of additive effects, recurrent selection should be useful in improving sheath rot resistance. According to Hallauer (2007), once additive gene effects are important, recurrent breeding methods that emphasizes on GCA and phenotypic selection should be used for improving targeted traits. As additive genes are highly fixable (Dabholkar, 2006), the best combiners found in this study are potential candidates for cultivar improvement programmes.

Because heritability is a measure of the heritable portion of variability, a higher heritability is an indication that the expression of targeted trait is mainly due to the additive gene effect, and selection should focus on phenotypic performance (Brown et al., 2014). This is in the same line with Abney, McPeek, and Ober (2001) who stated that with the absence of dominance and epistatic effects, narrow sense heritability is always equal to or less than the broad sense heritability. The present study revealed heritability level ranging from 63.7 to 89.2% for both broad and narrow sense, and therefore, LS, AUDPC and PE were highly heritable. The broad and narrow sense heritability estimates were equal for LS and AUDPC in this study, and this reflects the strong relationship between both traits.

High heritability estimates for PE corroborates with results reported by Sellammal, Robin, and Raveendran (2014) and are, slightly, in contrast to Cruz, Milach, and Federizzi (2008) and Girish et al. (2006), who reported moderate estimates of heritability.

As a significant maternal effect implies a difference in selection of a female parent for a particular crossing, this is not the case with the current study where maternal effects were not significant.

The level of dominance estimated in this study ranged between 0 and 1 except for PE when estimated based on male parents. This indicates partial dominance of genes involved in resistance to ShR, and consequently dominant genes were most important in number than recessive ones. The evidence of predominance of additive genetic effect on inheritance of resistance to ShR coupled with the predominance of dominant genes over recessive ones pave the way for a possibility of improving the resistance by introgression of resistance genes through recurrent selection or series of backcrossing.

5 | CONCLUSION

The analysis of the NCD II revealed significant general and specific combining ability estimates for LS, AUDPC and PE. Hence, both additive and non-additive gene effects were important in the

mechanisms governing inheritance of resistance to ShR with predominance of additive gene effects over non-additive gene effects. The analysis of level of dominance revealed the importance of partial dominant genes over recessive genes. The existence of additive gene effects coupled with partial dominance of genes indicated that crop improvement programmes should be through the introgression of resistance genes into new varieties with recurrent selection strategies focusing mainly on best GCA of parental materials. Varieties like Cyicaro, Yunertian and Yunkeng which were found as best combiners should be considered as potential source of resistant genes. This should be followed by selecting the best progeny as parents for the next generation to obtain substantial future breeding gains.

Because little is known about the mode of action associated with mechanism of inheritance of resistance to sheath rot of rice, the results from this study are a tremendous breakthrough in the effort for breeding for resistance.

ACKNOWLEDGEMENTS

The Alliance for Green Revolution in Africa (AGRA), African Center for Crop Improvement (ACCI) and University of KwaZulu-Natal are gratefully acknowledged for funding and supervising this study. Special thanks go also to Rwanda Agriculture Board (RAB) for facilitating this study in one way or another.

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How to cite this article: Mvuyekure SM, Sibiya J, Derera J, Nzungize J, Nkima G. Genetic analysis of mechanisms associated with inheritance of resistance to sheath rot of rice. *Plant Breed*. 2017;136:509–515. https://doi.org/10.1111/pbr.12492