

# Combining Ability Analysis of Blast Disease Resistance and Agronomic Traits in Finger Millet [*Eleusine coracana* (L.) Gaertn]

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## Abstract

Blast disease is the most important biotic constraint to finger millet production. Therefore disease resistant varieties are required. However, there is limited information on combining ability for resistance and indeed other agronomic traits of the germplasm in Uganda. This study was carried out to estimate the combining ability and gene effects controlling blast disease resistance and selected agronomic traits in finger millet. Thirty six crosses were generated from a  $9 \times 9$  half diallel mating design. The seed from the 36  $F_1$  crosses were advanced by selfing and the  $F_2$  families and their parents were evaluated in three replications. General combining ability (GCA) for head blast resistance and the other agronomic traits were all highly significant ( $p \leq 0.01$ ), whereas specific combining ability (SCA) was highly significant for all traits except grain yield and grain mass head<sup>-1</sup>. On partitioning the mean sum of squares, the GCA values ranged from 31.65% to 53.05% for head blast incidence and severity respectively, and 36.18% to 77.22% for the other agronomic traits measured. Additive gene effects were found to be predominant for head blast severity, days to 50% flowering, grain yield, number of productive tillers plant<sup>-1</sup>, grain mass head<sup>-1</sup>, plant height and panicle length. Non-additive gene action was predominant for number of fingers head<sup>-1</sup>, finger width and panicle width. The parents which contributed towards high yield were *Seremi 2*, *Achaki*, *Otunduru*, *Bulo* and *Amumwari*. Generally, highly significant additive gene action implied that progress would be made through selection whereas non-additive gene action could slow selection progress and indicated selection in the later generations.

**Keywords:** combining ability, finger millet, grain yield, gene action, head blast disease

## 1. Introduction

Finger millet production is faced with many biotic challenges; the most important of them being blast disease caused by *Pyricularia grisea* (Cooke) Sacc. There have been attempts to address this challenge resulting in some ephemeral solutions. *Pyricularia grisea* can cause yield losses as high as 50% on finger millet (Lenne et al., 2007) and in favourable seasons the losses can be as high as 90% (Esele, 1993). In Uganda, finger millet blast is endemic to all growing areas although some cultivars are more susceptible than others (Takan et al., 2004) and more severe in some areas than others depending on weather conditions. Despite its wide prevalence very little is actually known about host plant resistance and its inheritance compared to rice for instance. Blast appears on all plant parts damaging leaves, stems, peduncle and heads, with head blast the most destructive as it directly reduces yield (Prabhu, Filippi, & Zimmermann, 1996). Although chemical control has been shown to be effective (Bua & Adipala, 1995; Seetharam & Ravikumar, 1993), its use on a field scale is not practical because of resource constraints of the farmers growing finger millet making exploitation of host plant resistance an extremely important option in preventing yield loss and enhancing yields.

The gene action conditioning resistance to finger millet blast disease is not fully understood and similarly no information exists on the combining abilities of finger millet lines adapted to tropical conditions in Uganda under finger millet blast pressure. There however, exists some information especially from India and extensive

work on rice. Generation of such information would be useful in selecting parents in a breeding programme and choosing appropriate breeding procedures. Studies elsewhere have identified finger millet genotypes with resistance to *Pyricularia grisea* (Cooke) Sacc. (Shailaja, Thirumeni, Paramasivam, & Ramanadane, 2010; Krishnappa, Ramesh, Chandraprakash, Bharathi, & Doss, 2009; Takan et al., 2004) indicating that breeding for resistance is a realistic option. This can form the basis for initiating studies to determine the genetics of resistance to blast disease pathogen and later be able to incorporate this resistance in new cultivars with appropriate agronomic and farmer preferred attributes.

The main objectives of the current study were to assess the nature and magnitude of gene action controlling blast disease inheritance and other agronomic traits important to yield determination and to suggest breeding strategies for finger millet improvement. The specific objectives were to: (i) estimate the general combining ability (GCA) of selected parents and the specific combining ability (SCA) of a parent in a cross with another parent, and (ii) determine the genetic effects which control the inheritance of blast disease resistance and selected agronomic traits in finger millet.

## 2. Materials and Methods

### 2.1 Selection of Parental Materials

The experimental material consisted of nine finger millet varieties (Table 1) as parents. The varieties selected were adapted landraces, bred and released varieties and introductions from ICRISAT. The landraces and released cultivars used are highly popular among the farmers and are being used in various production systems. Owing to their already high adaptability, acceptability, resistance to blast disease (in some cases) and yielding ability, these were chosen for hybridization to exploit the existing variation for finger millet improvement in Uganda. Among the nine varieties, five had green pigmentation whereas four had purple pigmentation at the nodes and leaf margin (Table 1). These were deliberately selected so that the F<sub>1</sub>s could easily be identified as the purple pigmentation is known to be dominant over the green pigmentation (Shailaja, Thirumeni, Paramasivam, & Ramanadane, 2010; Krishnappa, Ramesh, Chandraprakash, Bharathi, & Doss, 2009) which served as a useful marker in identifying true crosses at the seedling stage where the parents had different nodal and head pigmentation. Other added markers were plant height, head shapes and seedling vigour.

### 2.2 Crossing Procedures

Finger millet is predominantly a self-pollinated crop with bisexual flowers (florets) which are small in size making artificial hybridization a difficult process. Emasculation without injury to floral parts is extremely difficult hence two methods were adopted for this study to improve chances of success.

Table 1. Parental lines with entry numbers, reaction to head blast disease, nodal pigmentation, head shapes and germplasm source

Entry	Type of disease reaction†	Nodal pigmentation	Head shapes	Source
01 (E11)	S	Purple	Open	ICRISAT
02 (ACF 5)	S	Green	Incurved	Introduction – world collection
03 (Seremi 2)	R	Purple	Semi compact	Released cultivar
04 (ACF 19)	R	Green	Tips curved	Introduction – world collection
05 (Achaki)	R	Green	Compact	Landrace – Tororo
06 (Abao)	MR	Purple	Compact	Landrace – Lira
07 (Otunduru)	MR	Purple	Compact	Landrace – Kaberamaido
08 (Bulo)	MR	Green	Tip curved	Landrace – West
09 (Amumwari)	R	Green	Open	Landrace – Busia

Note. † S = resistant, R = resistant, MR = moderately resistant.

The two methods were: 1) the polythene bag method (in which emasculation was obtained using a 7.5 cm × 10 cm polythene bag lined with moist filter paper inverted over the flower and plugged with absorbent cotton wool. This creates high humidity inside the bag. Under such humidity, the florets open, the anthers emerge but shed no pollen. Pollen was collected from the designated male parents by tapping the bag before dehiscence of anthers. The pollen collected from the bag was dusted on the emasculated head and again covered with a pollination bag and labeled; 2) The contact method of crossing as described by Ravikumar (1988) and successfully used by

Ratnakar, Mallikarjuna, Naveen-Kumar, and Jayarame-Gowda (2009) were adopted to obtain  $F_1$  seed. In this second method the heads of the male and female parents were brought together and finger to finger contacts were made by tying them together with a thread just before anthesis. Anthesis is known to take place from 1 am to 4 am and ends by 11 am (Ratnakar, Mallikarjuna, Naveen-Kumar, & Jayarame-Gowda, 2009). After pollination, ear heads were separated and seeds collected only from the female parent. This method is known to enhance the frequency of out-crossing by providing an opportunity for the pollen of male parents to come in close contact with the stigmatic surface of female parents.

### 2.3 Diallel Crosses and Evaluation of the Parents and Progenies

The nine selected parents were crossed in a green house at NaSARRI (Latitude  $1^{\circ}29'39''N$  Longitude  $33^{\circ}27'19''E$  1085 m.a.s.l.) using the  $9 \times 9$  half diallel mating design. The successful  $F_{1S}$  were identified in the field during the following season by comparing the crosses with the maternal parents. This was done by sowing the  $F_1$  seed between rows of both parents and among the crosses, plants similar to female parents were identified and removed based on the morphological markers. The true  $F_1$  plants were then advanced to obtain  $F_2$  seed. The  $F_2$  seed was sown under natural infestation in the field alongside the parents in an alpha-lattice design of  $5 \times 9$  by adopting a spacing of  $30 \text{ cm} \times 10 \text{ cm}$  between rows and plants in a single row. Basal application of diammonium phosphate fertilizer and top-dressing with urea was used to boost the nitrogen levels to facilitate disease development (Prabhu, Filippi, & Zimmermann, 1996; Seetharam & Ravikumar, 1993; Russell, 1978). Fourty competitive plants were labelled per plot from which data were recorded.

### 2.4 Data Collection

Data was collected on the following traits: head blast incidence and head blast severity under natural infestation, days to 50% flowering, number of productive tillers per plant, finger number per head, grain mass per head, plant height, finger length, finger width, panicle length, panicle width and grain yield  $\text{ha}^{-1}$ . Data on these traits were collected using finger millet descriptors (IBPGR, 1985) as a guide.

Grain yield ( $\text{tons ha}^{-1}$ ): measured as grain mass was taken from the forty plants, post-harvest and converted to  $\text{tons ha}^{-1}$ . Using the formula:

$$\text{Grain yield (tons ha}^{-1}\text{)} = \frac{333,333 \times \text{Yeild of the 40 plants (Kg)}}{40 \times 1000} \quad (1)$$

Head blast incidence and severity were recorded at the time of grain maturity. The disease incidence was calculated as the number of diseased plants divided by the total number of plants sampled per plot, whereas for severity, all heads from the forty plants were used to determine blast severity at maturity. For each head, proportions of spikelets affected by the disease were estimated and a Standard Evaluation System (SES) (IRRI, 1996) was adopted based on the number of heads, and head blast severity. The plants were then categorised as: 0 = no disease or immune, less than 10% = highly resistant, 11-20% = resistant, 20-30% = moderately resistant, 30-50% = susceptible and more than 50% highly susceptible.

### 2.5 Analysis

Data were analysed as a randomized complete block design (RCBD) since preliminary Lattice analysis resulted in no gain in accuracy due to blocking over RCBD analysis. Genetic analysis for blast disease resistance and other agronomic traits were performed as fixed effects model for the 45 entries (36 crosses and nine parents) in three replications. Diallel SAS05 programme was used to perform Griffings method 2, model I diallel analysis (Zhang, Kang, & Lamkey, 2005). This model was most suitable for the present study where only parents and one set of  $F_{1S}$  (without reciprocals) were included and treated as fixed effects in the analysis. From the mean sums of squares, estimates of GCA effects ( $g_i$ ) for each parent and SCA effect ( $s_{ij}$ ) for each cross combination were also determined. The statistical model for the mean value of a cross ( $i \times j$ ) is as follows:

$$Y_{ij} = \mu + g_i + g_j + s_{ij} + 1/b \sum_k \sum_l e_{ijkl} \quad (2)$$

Where,

$Y_{ij}$  = Mean of ( $i \times j$ )<sup>th</sup> cross over replications  $k$  ( $k = 1, 2, \dots b$ );

$\mu$  = The population (general) mean;

$g_i$  and  $g_j$  = General combining ability (*g.c.a.*) effects of  $i^{\text{th}}$  and  $j^{\text{th}}$  parents, respectively;

$s_{ij}$  = Specific combining ability (*s.c.a*) effect of  $ij^{\text{th}}$  cross such that  $s_{ij} = s_{ji}$ ;

$e_{ijkl}$  = Environmental effect associated with  $ijkl^{\text{th}}$  observation in  $k^{\text{th}}$  replication.

Restrictions are imposed on combining ability effects, such that  $\sum_i g_i = 0$  and  $\sum_i s_{ij} = 0$  (for each j) therefore,  $1/b \cdot \sum_k \sum_l e_{ijkl} = \text{Mean error effect}$ .

The relative importance of general and specific combining ability in determining progeny performance was assessed by calculating the proportion of GCA: GCA + SCA sum of squares. The GCA: GCA + SCA sum of square ratio was proposed by Sprague and Tatum (1942) (cited and used by Simmonds & Smartt, 1999).

### 3. Results

The mean of the parental lines for blast disease incidence, severity and grain yield plant<sup>-1</sup> are presented in Table 2. The nine parental lines showed significant differences in the reaction to head blast disease indicated by both incidence and severity, and grain yield. There was a whole range of reaction from resistance based on classification used here to susceptible being exhibited by parental lines *E 11* and *ACF 5* both of which were introductions from ICRISAT and collections at University of KwaZulu Natal respectively.

Table 2. Means of parental lines for head blast incidence, severity and grain yield (tons ha<sup>-1</sup>)

Entry	Head blast incidence (%)	Head blast severity (%)	Type of disease reaction‡	Grain yield (tons ha <sup>-1</sup> )
01 (E11)	68.7	34.0	S	1.36
02 (ACF 5)	52.6	57.0	HS	1.41
03 (Seremi 2)	31.0	16.7	R	2.61
04 (ACF 19)	30.7	18.0	R	2.94
05 (Achaki)	25.3	12.7	R	4.17
06 (Abao)	38.7	26.0	MR	2.30
07 (Otunduru)	24.3	26.7	MR	2.89
08 (Bulo)	27.0	28.7	MR	3.46
09 (Amumwari)	30.0	19.7	R	3.40
Mean	36.5	26.9		2.73
Minimum	18.0	11.00		1.11
Maximum	93.0	50.90		4.49
LSD (0.05)	8.58	5.71		0.26
C.V. (%)	31.7	28.2		10.8

Note. ‡ type of disease reaction: S = Susceptible, HS = Highly susceptible, R = Resistant and MR = Moderately resistant.

#### 3.1 Combining Ability Estimates

Results of mean sum of squares for blast disease incidence, severity and agronomic traits are presented in Table 3. The mean sum of squares for entry, GCA effects and SCA effects for head blast incidence and severity were highly significant ( $p \leq 0.01$ ) and partitioning the cross sum of squares the GCA effects of head blast incidence and severity accounted for 31.65% and 53.05% respectively.

Mean sum of squares for the other agronomic traits were all highly significant ( $p \leq 0.01$ ) for entry and GCA effects, whereas SCA effects were highly significant for all traits except panicle width which was just significant ( $p \leq 0.05$ ). Specific combining ability effects were non-significant ( $p \leq 0.05$ ) for grain mass head<sup>-1</sup> and grain yield ha<sup>-1</sup>. On partitioning the mean sums of squares, the GCA effects ranged from 36.18%-77.22%, whereas SCA effects contributed 22.78-63.82% of the total variance among the crosses. The contribution of GCA effects was highest for days to 50% flowering and lowest in panicle width, contrary to SCA effects. Considering all the agronomic traits; SCA effects were predominant for: number of fingers head<sup>-1</sup>, finger width and panicle width, whereas GCA effects were predominant for grain yield ha<sup>-1</sup>, days to 50% flowering, number of productive tillers plant<sup>-1</sup>, grain mass head<sup>-1</sup>, plant height and panicle length.

Table 3. Mean sum of squares for blast disease incidence, severity and other agronomic traits of finger millet in half diallel cross evaluated at NaSARRI

Source of variation	DF	FBI	FBS	Grain yield (tons ha <sup>-1</sup> )	Days to 50% flowering	Tillers plant <sup>-1</sup>	Finger number head <sup>-1</sup>	Grain mass head <sup>-1</sup>	Plant height	FL	FW	PANW	PANL
Rep	2	112.13 <sup>ns</sup>	45.97 <sup>ns</sup>	0.83 <sup>ns</sup>	11.34*	0.92*	0.39 <sup>ns</sup>	0.30 <sup>ns</sup>	173.41**	0.10 <sup>ns</sup>	0.02**	1.32**	0.26 <sup>ns</sup>
Entry	44	382.53***	345.54***	1.93***	53.67**	1.20***	1.15**	0.70***	161.94**	1.20**	0.02**	0.12**	1.46**
GCA	8	665.97**	1008.08**	6.85***	227.94**	3.57**	2.74**	2.50**	653.37**	3.23**	0.03**	0.25**	4.41***
SCA	36	319.54***	198.31**	0.82 <sup>ns</sup>	14.95**	0.67**	0.79**	0.29 <sup>ns</sup>	52.73**	0.75**	0.01**	0.10*	0.80**
Error	88	85.50	37.97	0.61	2.65	0.09	0.13	0.22	9.52	0.11	0.002	0.06	0.11
CV		27.47	22.83	11.25	2.22	11.49	5.41	24.33	4.07	5.57	5.22	11.99	5.25
R <sup>2</sup>		0.69	0.82	0.73	0.91	0.87	0.82	0.62	0.90	0.84	0.82	0.61	0.87
Corrected total	134												
Contribution of GCA		31.65	53.05	65.53	77.22	54.14	43.47	65.40	73.36	49.03	36.46	36.18	54.98
Contribution of SCA		68.35	46.95	34.57	22.78	45.86	56.53	34.60	26.64	50.97	63.54	63.82	45.02

Note. \*, \*\*, and \*\*\* indicates the term is significant at  $p \leq 0.05$ ,  $p \leq 0.01$  and  $p \leq 0.001$  respectively; ns – not significant ( $p > 0.05$ ), FBI = finger blast incidence, FBS = finger blast severity, FL = finger length, FW = finger width, PANW = panicle width, PANL = panicle length.

### 3.2. General Combining Ability Effects of the Parental Materials

The GCA effects for the nine parental lines for head blast disease and other agronomic traits are presented in Table 4. For head blast disease the desirable GCA effect for the parents should be negative. The GCA effects for head blast disease incidence were significantly positive for *E 11* ( $p \leq 0.01$ ), *ACF 5*, ( $p \leq 0.001$ ) and *ACF 19* ( $p \leq 0.05$ ), while negative, significant effects were shown for *Achaki* ( $p \leq 0.001$ ) and *Otunduru* ( $p \leq 0.01$ ), whereas, *Seremi 2*, *Abao*, *Bulo* and *Amumwari* were negative though non-significant ( $p \leq 0.05$ ). For blast severity, positive significant effects were recorded for parents: *E 11* ( $p \leq 0.001$ ), *ACF 5* ( $p \leq 0.001$ ) and ( $P \leq 0.05$ ). The parental materials produced similar effects (in terms of sign) for both incidence and severity. Negative significant effects were observed for *Seremi 2* ( $p \leq 0.001$ ), *Achaki* ( $p \leq 0.001$ ), and *Amumwari* ( $p \leq 0.001$ ) while *Otunduru* and *Bulo* showed non-significant ( $p \leq 0.05$ ), negative effect and *Abao* a positive, non-significant ( $p \leq 0.05$ ) effect. The results therefore indicated that the desirable parents were *Seremi 2*, *Achaki*, *Amumwari* and to some extent *Otunduru* and *Bulo*.

For grain yield ha<sup>-1</sup>, grain mass head<sup>-1</sup>, tillers plant<sup>-1</sup>, number of fingers head<sup>-1</sup>, finger length, finger width, panicle length and panicle width the desirable GCA effect was positive. Whereas desirable GCA effects for days to 50% flowering and plant height is negative. Parents with significant, positive GCA effects for grain yield ha<sup>-1</sup> were *Seremi 2*, *Achaki*, *Otunduru*, *Bulo* and *Amumwari*, whereas, for grain mass head<sup>-1</sup> were *Seremi 2*, *Achaki*, *Otunduru* and *Bulo*. Desirable combiners for productive tillers plant<sup>-1</sup> were *E 11*, *Achaki* and *Amumwari*; for number of fingers head<sup>-1</sup>, *Seremi 2*, *ACF 19*, *Achaki*, *Abao* and *Bulo*; while finger length had *E 11*, *Seremi 2*, *Achaki* and *Bulo*. Parents that showed negative, significant GCA effects for days to 50% flowering and therefore desirable were *E 11* and *Seremi*, whilst negative, high significant GCA effects ( $p \leq 0.01$ ) on plant height were recorded for *E 11*, *ACF 5*, *Seremi 2*, and *Abao*, while *Bulo* had no significant ( $p \leq 0.05$ ) GCA effect.

Table 4. General combining ability effects for blast disease and other agronomic traits

Parent	FBI	FBS	Grain yield (tons ha <sup>-1</sup> )	Days to 50% flowering	Tillers plant <sup>-1</sup>	Finger number head <sup>-1</sup>	Grain mass head <sup>-1</sup>	Plant height	FL	LFW	PANW	PANL
1	4.21**	3.67***	-0.72***	-5.57***	0.37***	-0.60***	-0.43***	-4.01***	0.22***	-0.06***	0.13**	0.57***
2	7.91***	11.02***	-0.53***	0.67*	-0.42***	0.11	-0.32***	-4.58***	-0.20**	-0.03***	0.05	-0.35***
3	-2.99	-5.70***	0.29*	-3.05***	-0.32***	0.21**	0.17*	-6.44***	0.28***	0.01	-0.04	-0.07
4	3.15*	2.20*	-0.26*	1.19***	-0.19**	0.16*	-0.15	2.09***	-0.15**	0.01	-0.07	-0.04
5	-6.15***	-7.05***	0.54***	0.86**	0.48***	0.16**	0.33***	4.79***	0.47***	0.02*	0.16**	0.57***
6	0.91	1.80	-0.31	-0.02	-0.09	0.16**	-0.19*	-1.85**	-0.53***	-0.02**	-0.06	-0.37***
7	-4.45**	-1.23	0.35**	1.91***	-0.05	-0.33***	0.21**	5.19***	-0.12*	0.01	-0.03	-0.28**
8	-1.73	-0.54	0.42**	1.46***	-0.17**	0.23***	0.25**	0.11	0.20**	0.04***	0.07	0.19**
9	-0.87	-4.18***	0.21	2.55***	0.39***	-0.09	0.13	4.71***	-0.17**	0.03**	0.05	-0.21**
SE	9.24	6.15	0.28	1.63	0.30	0.36	0.47	3.08	0.34	0.04	0.24	0.33

Note. \*, \*\*, and \*\*\* indicates the term is significant at  $p \leq 0.05$ ,  $p \leq 0.01$  and  $p \leq 0.001$  respectively; FBI = finger blast incidence, FBS = finger blast severity, FL = finger length, LFW = longest finger width, PANW = panicle width, PANL = panicle length. Parents 1, 2, 3, 4, 5, 6 and 7 are: E 11, ACF 5, Seremi 2, ACF 19, Achaki, Abao, Otunduru, Bulu and Amumwari respectively.

#### 4. Discussion

The results indicated a high range for both blast disease incidence and severity which probably implied continuous variation exhibited by the genotypes in terms of head blast resistance. This may point to polygenic control, coupled with the fact that no cultivar showed or approached immunity. Some of the varieties showed high levels of resistance which may provide economically acceptable control of the disease and therefore could be used as sources of resistance in combination with other analysis results.

##### 4.1 Combining Ability Effects and Gene Action

The significant GCA and SCA effects observed for both head blast severity and incidence showed that both additive and non-additive gene effects were important to head blast resistance. The GCA effects accounted for most of the head blast severity variance whereas the SCA effects contributed most of the head blast incidence variance based on cross sums of squares, an indication that selection of parents can contribute to progress for blast severity. Similar findings were reported by Seetharam and Ravikumar (1993) on severity, but completely in contrast to that of Selvaraj, Nagarajan, Thiyagarajan, Bharathi, and Rabindran (2011) on rice panicle blast. The variance to the results of Seetharam and Ravikumar (1993) on incidence, and Selvaraj, Nagarajan, Thiyagarajan, Bharathi, and Rabindran (2011) on both incidence and severity may point to the fact that the mechanisms of resistance depend on the germplasm used and environment where investigations are carried out as was also reported by Ravikumar (1988). The current results showed that additive gene action was more predominant for head blast severity while non-additive gene action was more predominant for head blast incidence, an indication of severity being fairly heritable whereas incidence is less heritable and making progress would be slow. The presence of greater additive genetic variance for severity would also suggest that disease reaction for progeny families is predictable based on the GCA estimates of its parents (Falconer & Mackay, 1996; Dhillon, 1975). In contrast, the presence of greater non-additive genetic variance as exhibited in incidence makes it less predictable and would slow progress to selection for incidence.

The results further showed preponderance of additive gene action for grain yield, days to 50% flowering, tillering ability, grain mass head<sup>-1</sup>, plant height and panicle length except for finger number head<sup>-1</sup>, finger width and panicle width; a suggestion that both additive and non-additive gene actions and/or variations are important. Similar results were obtained by Parashuram, Gowda, Satish, and Mallikarjun (2011) for number of fingers head<sup>-1</sup>, finger width, and panicle width but contrary for the other agronomic traits in the current study, and completely contrary to report by Shailaja, Thirumeni, Paramasivam, and Ramanadane (2010) whose report indicated non-significance for these traits under salinity conditions further augmenting the importance of environmental conditions on expression of these traits in finger millet.

Based on the results of these investigations, additive gene effects were more important in transmission of blast resistance, number of productive tillers, days to 50% flowering, grain mass per head, plant height and panicle

length. This implies that breeding progress can be achieved through selection for these traits. Selection for these traits therefore would involve breeding methods that entail selection in the early generations such as single seed descent, pedigree selection and modified pedigree as suggested in rice by Hammoud, Sedeek, El-Rewainy, and El-Namaky (2012). In finger millet specifically, Andrews (1993) suggested a method that involves bulking before evaluation as an appropriate method. In situations where non-additive gene effects are more important, selection should be delayed until later generations as the case was for finger and panicle width. For these traits repeated crossing in the segregating populations may be useful to pool all the desirable genes in one genotype as proposed by Selvaraj, Nagarajan, Thiyagarajan, Bharathi, and Rabindran (2011).

#### 4.2 General Combining Ability Effects of Parents for Blast Reaction and Yield Traits

The selection of parents based on *per se* performance may not always result in producing superior crosses (Simmonds & Smartt, 1999; Falconer & Mackay, 1996), and they pointed out that combining ability of parents gives useful information on the choice of parents in terms of expected performance of their progenies. This was clearly shown in cases where the magnitude and sign of the effect of each parent was not in agreement with individual performance. In the current investigations, most resistant parents to blast disease infection included *Achaki*, *Seremi 2*, *ACF 19*, and *Amumwari*. Of these parental materials, *Achaki*, *Seremi 2*, and *Amumwari* had negative, significant GCA effects which were desirable for blast resistance showing their capacity to transmit resistance for head blast disease. However, *ACF 19* in spite of being resistant, showed positive, significant ( $p \leq 0.05$ ) GCA effects for both head blast incidence and severity implying it would contribute towards susceptibility in most of the progeny families for which it is involved unlike the other three parental lines, therefore, it is not appropriate for incorporation in blast resistance breeding. Furthermore, in the current study, *Otunduru*, which exhibited moderate resistance had a negative, highly significant ( $p \leq 0.01$ ) GCA effect for head blast incidence and significant, negative SCA effect for blast disease in its progeny families with *E 11* a susceptible material, *Seremi 2* and *Amumwari* whilst positive, significant SCA effect in crosses with *ACF 5*, and *Abao*. It is suffice to suggest that *Otunduru*, unlike *ACF 19* is appropriate for incorporation in blast resistance breeding.

Parents that had positive significant GCA effects for grain yield contributed towards higher yields in most of the progenies in which they were part. For days to 50% flowering, negative, significant GCA effects indicated early maturity and these were observed for *E 11* and *Seremi 2*. Likewise desirable height was depicted by significant, negative GCA effects as was observed with *E 11*, *ACF 5*, *Seremi 2* and *Abao*. Positive, significant GCA effects for days to 50% flowering indicated late maturity; however, overall these results are indications that parents with good combining ability for grain yield per plant but were late maturing as depicted by positive, significant GCA effects for days to 50% flowering may be suited for high resource (potential) areas. It is also possible to select lines with positive GCA effects for yield and negative GCA effects for days to 50% flowering for limited resource (low potential) areas as they may also escape drought. Moreover they could also be used to generate early maturing cultivars suitable for increasing cropping intensity for the high potential areas. Meanwhile desirability of negative effects for height is to avoid lodging, which would even further be enhanced in high potential areas.

Knowledge of combining ability with mean performance of parents is therefore of great value in selecting suitable parents for hybridization programme (Selvaraj, Nagarajan, Thiyagarajan, Bharathi, & Rabindran, 2011; Simmonds & Smartt, 1999). In the current study, high values for mean performance (in terms of grain yield) and GCA effects observed in some parental lines is clearly evident and this was also observed by Parashuram, Gowda, Satish, and Mallikarjun (2011). Parents *Seremi 2*, *Achaki*, *Otunduru* and *Amumwari* recorded high mean performance and GCA effects for yield contributing traits studied and blast disease resistance and, therefore, will be pertinent in the hybridization programme for selection of superior recombinants. Parashuram, Gowda, Satish, and Mallikarjun (2011); Tamilcovane and Jayaraman (1994); and Ravikumar, Shankare-Gowda & Seetharam (1986) also identified good general combiners in finger millet in India.

#### 5. Conclusion

In conclusion parental materials that were resistant to head blast disease observed in the study included *Achaki*, *Seremi 2*, *ACF 19*, *Otunduru* and *Amumwari*, the parents *Achaki*, *Seremi 2*, and *Amumwari* had negative GCA effects and contributed negative SCA effects in most of the crosses involving them indicating that they are potential parents for head blast resistance breeding. Parental materials *Achaki*, *Seremi 2*, *Otunduru*, *Bulo* and *Amumwari* contributed towards high grain yield and with exception of *Seremi 2* were late in maturity. General combining ability contributed 31.65% and 53.05% of the crosses sums of squares for blast incidence and severity respectively while SCA effects contributed 68.35% and 46.95% respectively. The GCA effects for grain yield, days to 50% flowering and plant height accounted for 65.5%, 77.22% and 73.36% respectively of the crosses

sums of squares. This indicated the predominance of genes with additive gene effects for grain yield ha<sup>-1</sup>, days to 50% flowering and plant height in the parental lines and by extension high heritability for these traits in finger millet. Overall, highly significant additive effects implied that progress in high grain yield and blast disease resistance would be made through methods such as pedigree breeding and modified pedigree.

## References

- Andrews, D. J. (1993). Principles for breeding small millets. In K. W. Riley, S. C. Gupta, A. Seetharam, & J. Mushonga (Eds.), *Advances in small millets* (pp. 411-423). International Science Publisher, New York, USA.
- Bua, B., & Adipala, E. (1995). Relationship between head blast severity and yield of finger millet. *International Journal of Pest Management*, 41, 55-59. <http://dx.doi.org/10.1080/09670879509371922>
- Dhillon, B. S. (1975). The application of partial-diallel crosses in plant breeding: A review. *Crop Improvement*, 2, 1-8.
- Esele, J. P. (1993). The current status of research on finger millet blast disease (*Pyricularia grisea*) at Serere research station. In K. W. Riley, S. C. Gupta, A. Seetharam, & J. Mushonga (Eds.), *Advances in small millets* (pp. 467-468). International Science Publisher, New York.
- Falconer, D. S., & Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th ed.). Longman Group Ltd, United Kingdom.
- Griffings, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, 9, 463-493. <http://dx.doi.org/10.1071/BI9560463>
- Hammoud, S. A. A., Sedeek, S. E. M., El-Rewainy, I. O. M., & El-Namaky, R. A. (2012). Genetic behaviour of some agronomic traits, blast disease and stem borer resistance in two rice crosses under two nitrogen levels. *Journal of Agricultural Research of Kafer El-Sheik University*, 38, 83-105.
- IBPGR (International Board for Plant Genetic Resources). (1985). *Descriptors of finger millet (Eleusine coracana (L.) Gaertn)* (p. 20). IBPGR Secretariat, Rome, Italy.
- IRRI. (1996). *Standard Evaluation System for Rice* (4th ed.). IRRI, INGER Genetic Resources Center, Manila, Philippines.
- Krishnappa, M., Ramesh, S., Chandraprakash, J., Bharathi, J. G., & Doss, D. D. (2009). Genetic analysis of economic traits in finger millet. *SAT eJournal*, 7, 1-5.
- Lenne, J. M., Takan, J. P., Mgonja, M. A., Manyasa, E. O., Kaloki, P., Wanyera, N., ... Sreenivasaprasad, S. (2007). Finger millet blast disease management. A key entry point for fighting malnutrition and poverty in East Africa. *Outlook on Agriculture*, 36, 101-108. <http://dx.doi.org/10.5367/000000007781159994>
- Parashuram, D. P., Gowda, J., Satish, R. G., & Mallikarjun, N. M. (2011). Heterosis and combining ability studies for yield and yield attributing characters in finger millet (*Eleusine coracana* (L.) Gaertn.). *Electronic Journal of Plant Breeding*, 2, 494-500.
- Prabhu, A. S., Filippi, M. C., & Zimmermann, F. P. (1996). Genetic control of blast in relation to nitrogen fertilization in upland rice. *Pesq. Agropec. Bras.*, 31, 339-347.
- Ratnakar, M. S., Mallikarjuna, N. M., Naveen-Kumar, K. S., & Jayarame-Gowda, M. V. (2009). Cytomorphological studies in inter-specific hybrids of finger millet. *Gregor Mendel Foundation Proceedings, 2009*, 69-74.
- Ravikumar, R. L. (1988). *Genetic and biochemical basis of blast resistance in finger millet (Eleusine coracana Gaertn.)* (PhD Thesis). University of Agricultural Sciences, Bangalore, India.
- Ravikumar, R. L., Shankare-Gowda, B. T., & Seetharam, A. (1986). Studies on Heterosis in finger millet. *Millet Newsletter*, 5, 26-27.
- Russell, G. E. (1978). *Plant breeding for pest and disease resistance*. Butterworth and Company Publisher, Ltd. London, UK.
- Seetharam, A., & Ravikumar, R. L. (1993). Blast resistance in finger millet – Its inheritance and biochemical nature. In K. W. Riley, S. C. Gupta, A. Seetharam, & J. Mushonga (Eds.), *Advances in small millets* (pp. 449-465). International Science Publisher, New York, USA.
- Selvaraj, C. I., Nagarajan, P., Thiyagarajan, K., Bharathi, M., & Rabindran, R. (2011). Studies on heterosis and combining ability of well known blast resistant rice genotypes with high yielding varieties of rice (*Oryza*



- sativa* L.). *International Journal of Plant Breeding and Genetic*, 5, 111-129. <http://dx.doi.org/10.3923/ijpbg.2011.111.129>
- Shailaja, H. B., Thirumeni, S., Paramasivam, K., & Ramanadane, T. (2010). Combining ability analysis in Finger millet *Eleusine coracana* (L.) Gaertn.) under salinity. *Electronic Journal of Plant Breeding*, 1, 129-139.
- Simmonds, N. W., & Smartt, J. (1999). *Principles of Crop Improvement* (2nd ed.). Blackwell Science Ltd., Oxford, UK.
- Takan, J. P., Akello, B., Esele, P., Manyasa, E. O., Obilana, A., Audi, P. O., ... Sreenivasaprasad, S. (2004). Finger millet blast pathogen diversity and management in East Africa: a summary of project activities and outputs. *International Sorghum and Millets Newsletter*, 45, 66-69.
- Tamilcovane, S., & Jayaraman, N. (1994). Association between yield components in ragi. *Journal of Phytological Research*, 7, 194-194.
- Zhang, Y., Kang, M. S., & Lamkey, K. R. (2005). DAILLEL-SAS05. A Comprehensive programme for Griffings and Gardner-Eberhart analyses. *Agronomy Journal*, 97, 1097-1106. <http://dx.doi.org/10.2134/agronj2004.0260>

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