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Combining Ability for Resistance to Maize Lethal Necrosis Disease in Kenya

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ABSTRACT

Maize is a natural host to more than 50 viruses including members of the Potyviridae group which in combination with Maize Chlorotic mottle virus (MCMV) cause maize lethal necrosis leading to high yield losses. A study involving an assortment of maize germplasm was used to estimate the genetic effects attributable to the resistance to maize lethal necrosis resistance. The maize genotypes were crossed in a North Carolina design II to generate 25 crosses. The parents and their derivative crosses were screened for their combining ability for MLN and associated disease parameters. Among the parents involved in the study, only one parent UON-2015-119 showed desirable GCA for all the traits implying diversity of the rest of the material involved. Thus, the good combiners for the different traits could be used to produce desirable transgressive segregants to maximize the disease resistance. For the SCA effects, UON-2015- 50/ UON-2015-109, UON-2015-50 /UON-2015-112 and UON-2015-50 / UON-2015- 113 showed good values for all the disease parameters. These elite crosses had the parent UON-2015- 50. The parent UON-2015- 50 showed poor GCA effects for all the disease parameters. Also, the parent UON-2015-119 showed poor SCA effects despite the desirable GCA effect for all the disease parameters. This implies that any breeding method chosen should first accumulate favourable genes in homozygous state while breaking the linkage blocks. Also, non additive gene action attributable to both additive x epistatic and dominance x dominance gene interaction could be responsible for the resistance to the MLN. The non additive gene action is also non allelic and produces over-dominance which is non fixable. These superior parents and crosses could be used to develop maize varieties to improve maize production in Kenya.

INTRODUCTION

Maize production in Kenya is greatly threatened by the maize lethal necrosis (MLN) disease which is caused by the synergistic interaction of the maize chlorotic mottle virus (MCMV) and sugarcane mosaic virus (SCMV). The MLN is characterized by chlorotic mottling of leaves, necrotic lesions, dead heart, sterile pollen, small cobs, or no seed set at all and even plant death. The maize crop offers a habitat to more than 50 viruses most of which are a major contributor to the low yields (Masuka *et al*., 2017; Zambrano *et al*., 2014). The Kenyan climatic conditions favour the thriving of the viruses coupled with the maize monoculture within the country. Extremely hot conditions cause mosaics, necrosis and stripes leading to reduction in the incubation period leading to rapid multiplication and spread of the viruses within susceptible varieties. In the moderately resistant varieties, the viruses move slowly from the foci of inoculation into the young leaves, roots, and the emerging leaves of the plant (Gemechu *et al*., 2004). Most of the currently grown maize varieties are highly susceptible to MLN putting maize production at stake. MLN could be managed through cultural methods, chemical control, and host resistance breeding. Cultural methods include the use of crop rotation whereby the farmers are advised to alternate their crop with non-cereal crops such as potatoes for at least two seasons. Practicing sanitation in the field could also help to reduce the pathogen and vector population (CABI, 2016). Under chemical management, focus is on the use of insecticides to control the vectors both for soil borne and early season vectors. Use of chemicals such as Thunder (Imidacloprid 100g) and bulldock (Beta – Cyfluthrin 0.5g/kg) is effective in controlling the vector carrying the pathogens. However, chemical method is not economically viable to most farmers since they are expensive, and most farmers cannot afford them. Thus, host resistance breeding aimed at identifying resistance sources presents the most feasible option to the resource constraint small scale farmers who form the bulk of the maize producers in Kenya. The development of bi-parental crosses and their evaluation under either hot spots or under natural infestation could enhance identification of promising resistance. However, a proper understanding of the elite germplasm population structure regarding their combining ability is imperative if any breeding efforts are to be efficient and to enable the realization of genetic gains (Kamara *et al*., 2014; Masuka *et al*., 2017).

The combining ability of any inbred line rests on its capacity to produce superior hybrids in combination with the other inbred lines (Salami and Agbowuro, 2016). Both the general and specific combining ability of the lines and progenies remain imperative in any meaningful breeding program. This implies that a breeder should establish whether the resistance to MLN is attributed to additive genetic variance or non additive genetic variance (dominance or epistatic deviations) (Kinfe *et al*., 2015). The GCA gives the breeding value of the parents and determines the future usefulness and commercial utilization of such parents in hybrid generation. Heterosis is also an important component to be considered in breeding efforts and the genetic material must have adequate genetic diversity which determines the choice of breeding method and the prediction of the hybrid performance. The nature of the gene action is also important in enhancing the expression of important traits (Abera *et al*., 2016).

The resistance to the MLN causal agents has been attributed to different types and number of genes. The involvement of a single gene, oligogenic genes with modifier effects and the existence of genotype by environment interaction have complicated the elucidation of the exact gene effects thus the efficient utilization of any identified resistance (Souza *et al*., 2008). Mapping studies have also revealed the presence of different loci conditioning resistance to the different viruses causing MLN (Souza *et al*., 2008). Previous efforts by the International Maize and Wheat Improvement Center (CIMMYT) and Kenya Agricultural and Livestock Research Organization (KALRO) have made great strides towards combating the threat posed by MLN (Semagn *et al*., 2014; Gowda *et al*., 2015; http://www.cimmyt.org). Previous research has also reported the involvement of genes with major, epistatic, and minor effects (Semagn *et al*., 2014; Wu *et al*., 2007). Non additive gene action associated with the effect of genotype by environment interaction has also been reported. Thus, to efficiently reduce yield losses associated with MLN, knowledge of the combining ability and gene action of any promising maize lines needs to be established. This will enable the efficient deployment and introgression of the resistance sources into adapted maize backgrounds to combat further maize yield losses. Thus, this study set out to achieve the following objectives: a) To estimate the general combining ability (GCA) and specific combining ability (SCA) of maize in respect to MLN resistance and b) To identify the best single cross hybrids with regard to the MLN resistance.

MATERIALS AND METHODS

Plant Materials

Ten maize genotypes were identified to have resistance to MLN at the Field Station of the University of Nairobi and at KALRO Naivasha during the 2015 – 2016 cropping seasons (Table 1). These were crossed in a North Carolina Design II (NCDII) mating design.

Table 1: List of genotypes used in the development of the F1 crosses following a North Carolina Design II

Parent	Accession	Entry designation	MLN score (across two seasons) (based on Sitta *et al*., 2017)
P1	UoN-2015-117	MLR-12 (Female)	3
P2	UoN-2015-49	MUG-49 (Female)	2
P3	UoN-2015-50	MUG-50 (Female)	2
P4	UoN-2015-119	MLR-14 (Female)	3
P5	UoN-2015-114	MLR-9 (Female)	3
P6	UoN-2015-116	MLR-11 (Male)	3
P7	UoN-2015-112	MLR-7 (Male)	3
P8	UoN-2015-113	MLR-8 (Male)	1
P9	UoN-2015-106	MLR-1 (Male)	3
P10	UoN-2015-109	MLR-4 (Male)	2

(UoN= University of Nairobi)

Experimental Design and Layout

Development of the F1 crosses

Each of the ten parents (Table 1) was planted in double rows at a spacing of 0.75 m inter-rows and 0.25 m intra-row spacing at KARLO-Kiboko. Two seeds were planted per hill and later thinned to one plant per hill. Diammonium Phosphate (DAP) fertilizer was applied during planting at the rate of 10 g/hill and Calcium ammonium nitrate (CAN) was used as a top dress at the rate of 10 g/hill. The field was kept weed free by hand hoe weeding. Before silk emergence, the ear shoots were covered with shoot bags to prevent contamination from unwanted pollen. The tassels were also bagged a day after the main branch started shedding pollen. Pollen was collected from bagged tassels and used to pollinate the emerged silk. After pollination, ears were covered by use of the pollen bags and stapled to ensure seed set and avoid any other contamination from foreign pollen.

Evaluation of the parents and F_1 population

The 25 F_1s, their parents and three local checks were grown in the greenhouse at the field station (Upper Kabete) of the University of Nairobi. The experiment was laid out following a completely randomized design (CRD) with three replicates. Two seeds were planted per hill and then thinned to one seedling after emergence. Each pot had four hills of the maize seeds. DAP fertilizer was used at a rate of 10grams per pot and the urea fertilizer was used during top dressing at the rate of 10 grams per pot.

Isolation of Pathogens, Preparation of Inocula and Inoculation

Maize chlorotic mottle virus (MCMV) and sugarcane mosaic virus (SCMV) were isolated from diseased tissue of maize leaves showing clear symptoms of MCMV and SCMV at National Agriculture Research Institute (NARI-KENYA) whereby the two viruses are maintained at the Biosafety Greenhouse (BGH). The leaves were cut into small pieces and stored in the freezer at a temperature of -20˚C. 0.1M of phosphate buffer was made by mixing potassium phosphate dibasic (Anhydrous) and Potassium dihydrogen orthophosphate (Potassium phosphate monobasic) to a pH of 7.0 using the following ratios: KH_2PO4 = 10.8g, K_2HPO_4 = 4.8g and Na_2SO_3 = 1.26 and Carborandum ($SiCO_3$) = 1g/l. Then 5g of leaves with MCMV and 25g of leaves with SCMV at a ratio of 1:5 were weighed and ground using sterile pestle and mortar to obtain homogenate solution. This solution was added to the buffer to make 300 ml. The combination of MCMV and SCMV inocula was rubbed onto the young leaves at the age of two weeks from germination. Carborandum ($SiCO_3$) was used to cause microscopic injury of the leaves for easy penetration of the virus. The second inoculation was done one week (7 days) later to ensure that there were no disease escapes.

Data collection

MLN disease assessment

Disease assessment methods used were objective and included disease severity and incidence.

The MLN disease severity was assessed by estimating the proportion of total photosynthetic area infected (Table 2). Disease severity scoring began one week after the repeat inoculation and repeated every seven days interval for a period of eight weeks. The delayed scoring for the presence of MLN was to detect late developing infections (Zambrano *et al*., 2013). The plants could grow to physiological maturity to get an indication of the effect of MLN on maturity and yielding potential of the maize genotypes.

Table 2: MLN disease severity assessment among the genotypes

MLN Score	Symptoms
1	No MLN symptoms
2	Fine chlorotic streaks
3	Chlorotic mottling
4	Excessive chlorotic mottling and some necrosis
5	Dead heart symptoms/complete plant death

Source (CIMMYT)

The MLN incidence was achieved by counting the number of leaves infected by MLN given as a percentage of the total number of leaves in the maize plant.

$$\text{Disease Incidence} = \frac{\text{Number of infected leaves}}{\text{Total Number of leaves on the maize plant}} \times 100$$

Data analysis

Area under disease progress curve (AUDPC)

The disease scores were converted into the area under disease progress curve (AUDPC) following Wilcoxson *et al*., (1975) method. AUDPC is simply the intensity of disease integrated between two times; it is a crucial quantitative summary of the disease intensity over time for comparison across years, locations as well as management tactics. The AUDPC expresses the dynamic of an epidemic as a single value. The different epidemics can be compared by normalizing the AUDPC value of each epidemic by calculating the relative area under disease progress curve (rAUDPC) (Wilcoxson *et al*., 1975).

$$AUDPC = \sum_{t=1}^{n-1} \left(\frac{yi + yi+1}{2} \right) (\text{ti} + 1 - \text{ti}) \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{Equation 1}$$

Where,

Nt =total number of observations, y*i* = injury intensity at the *i*th observation, *t* = time at the *i*th observation (Wilcoxson *et al*., 1975; Sitta *et al*., 2017).

Analysis of variance

Analysis of variance for the traits was done based on the model by Brigitte, (1999) following Equation 2. The mean comparison was done using the Fisher's protected least significant differences (LSD) at 5% significance level.

ANOVA model (Brigitte, 1999)

$Y_{ij} = \mu + t_i + r_j + e_{ij}$……Equation 2

Where, μ = the overall mean, $r_{i=}$ j^{th} replication effect, $t_{i=}$ i^{th} treatment effect, and $e_{ij=}$ error term

Combining ability estimates

The collected data were analyzed by SAS (Version 9.3) program. General combining ability (GCA) and specific combining ability (SCA) effects were estimated by the following formula by Singh and Chaundhary (1985).

For testing significance of GCA and SCA

SE (GCA for lines) = $\sqrt{(M_e / r \times m)}$
SE (GCA for testers) = $\sqrt{(M_e / r \times f)}$
SE (SCA effects) = $\sqrt{(M_e / r)}$

For calculation of CD

GCA: SE $(g_i - g_j)$ line=$\sqrt{(2\ M_e / r \times m)}$
GCA: SE $(g_i - g_j)$ tester=$\sqrt{(2\ M_e / r \times f)}$
SCA: SE $(s_{ij} - s_{kl})$ = =$\sqrt{(2\ M_e / r)}$
CD = SE difference × t value
Where, r, f and m = number of replications, female and male, respectively, SE = standard error of the estimate and M_e = error mean square.

Partitioning of combining ability estimates

Baker`s ratio (1978) was used for the estimation of the relative importance for the GCA and SCA by using Equation 3.

$$\frac{6^2_{GCA}(female) + 6^2_{GCA}(male)}{6^2_{GCA}(female) + 6^2_{GCA}(male) + 6^2_{SCA}} \quad \ldots\ldots\text{Equation 3}$$

Whereas,
6^2GCA (female) indicates variance components for general combining ability of female, 6^2GCA (male) indicates variance components for general combining

ability for male and σ^2SCA indicates the variance components for specific combining ability.

RESULTS

The parent UON-2015-119 showed good GCA effects for all the disease parameters assessed namely the percentage MLN incidence, the MLN severity scores and their AUDPC values. UON-2015-117 showed good GCA value for AUDPC values. Other parents who showed good GCA values for percentage MLN incidence included UON-2015-109, UON-2015-112. UON-2015-113 and UON-2015- 116 (Table 3).

Table 3: General Combining Ability effects for the parents evaluated for resistance to MLN in the greenhouse in two seasons

Parents	%MLN Incidence	MLN AUDPC	Final MLN score	MLN rAUDPC
UON-2015-117	5.3	-6.3	0.0	-4.1
UON-2015-119	-10.4	-10.2	-0.5	-6.7
UON-2015-49	0.0	0.5	0.3	0.4
UON-2015-50	4.3	4.1	0.4	2.8
UON-2015-109	-1.4	4.3	0.2	2.8
UON-2015-112	-0.1	0.4	0.3	0.2
UON-2015-113	-6.7	0.0	0.2	0.0
UON-2015- 116	-2.8	2.3	0.2	1.5

For the SCA effects, UON-2015- 50/ UON-2015-109, UON-2015-50 /UON-2015-112 and UON-2015-50 / UON-2015- 113 showed good values for all the disease parameters. These elite crosses had the parent UON-2015- 50. The crosses UON-2015- 117 / UON-2015- 109, UON-2015- 117/ UON-2015-112, UON-2015- 117 / UON-2015- 113 and UON-2015- 117 / UON-2015- 116 showed good SCA effects for the percentage MLN incidence (Table 4). The cross UON-2015- 49 / UON-2015- 112 showed good SCA effects for percentage MLN incidence and MLN severity score

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Table 4: Specific Combining Ability effects for the parents evaluated for resistance to MLN in the greenhouse in two seasons

Parents	%MLN Incidence	Final MLN score	MLN AUDPC	MLN rAUDPC
UON-2015- 117 / UON-2015- 109	-7.5	0	6.7	4.4
UON-2015- 117/ UON-2015-112	-0.1	0.4	23.1	15.2
UON-2015- 117 / UON-2015- 113	-11.7	-0.5	2	1.3
UON-2015- 117 / UON-2015- 116	-10.6	-0.3	16.6	10.9
UON-2015- 119 / UON-2015- 109	11.2	0.8	13.4	8.8
UON-2015- 119 / UON-2015- 112	11.7	0.9	20	13.2
UON-2015-119 / UON-2015- 113	9.5	0.3	6.1	3.9
UON-2015- 119 / UON-2015- 116	7	0.6	11.5	7.5
UON-2015- 49 / UON-2015- 109	-4.9	-0.6	3.6	2.4
UON-2015- 49 / UON-2015- 112	2.9	-0.4	-2.2	-1.4
UON-2015-49 / UON-2015- 113	6.6	-0.1	4.1	2.7
UON-2015-49 / UON-2015- 116	5.2	-0.1	4.8	3.2
UON-2015-50 / UON-2015-109	-3.7	-0.4	-13.9	-9.2
UON-2015-50 / UON-2015- 112	-13.9	-0.8	-15.4	-10.1
UON-2015- 50 / UON-2015-113	-6.9	-0.7	-21.1	-13.9
UON-2015-50 / UON-2015-116	6	0.3	13.4	8.8

DISCUSSION, CONCLUSION, AND IMPLICATION

The combining ability information helps to inform on the selection of best parents and nature and magnitude of involved gene action thus ensuring the effective utilization of genetic variation (Kiyyo and Kusolwa, 2017; Legesse *et al*., 2009). This allows the estimation of such effects without interference by linkage effects (Murtadha *et al*., 2016). Among the parents involved in the study, only one parent showed desirable GCA for all the disease parameters assessed. This implies the diversity of the rest of the material involved. Through the information from this study, exploitation of the resident variability will enable the discrimination of such variation among parents which could be highly related (Kiyyo and Kusolwa, 2017). Thus, the good combiners for the different traits could be used to produce desirable transgressive segregants to maximize the disease resistance. For disease resistance, a high negative GCA implies superiority of the parental mean to the general mean. Thus, there is a desirable gene flow from parents to offspring with high intensity associated with additive genes (Fasahat *et al*., 2016). The high GCA value also implies high heritability and less environmental influence (Fasahat *et al*., 2016). The exploitation of the parents with good GCA could lead to development of good open pollinated varieties, since populations with high frequency of favorable alleles are important sources for plant selection. The utilization of such elite parents in breeding programs will save time and resources in ensuring that only elite populations are used in producing superior crosses. The evaluation of the parents maximizes on the heterotic response. The use of genotypes with high combining ability will give superior hybrids and segregant populations with large genetic variability.

In general, populations with large GCA exhibited potential as parents of hybrid varieties, as well as for inclusion in breeding programs, since they may contribute superior alleles in new populations (Vacaro *et al*., 2002). The parent UON-2015-119 can be said to be highly adaptable regarding these disease parameters. GCA determines the best lines to be used as parents in a crop improvement program and this helps breeders to combine such desirable genes found in different genotypes. Also, there is a high probability of getting superior hybrids when superior inbred lines are used. This is enabled by the fact that favourable alleles are accumulated through selection (Asea *et al*., 2012). GCA is controlled by genetic material, is heritable and can be transmitted to the offspring enabling steady genetic gain in plant breeding. The involvement of the NCDII enables the determination of maternal effects and calculation of heritability based on male variance, which is free from maternal effects (Fasahat *et al*., 2016). Parents with good GCA imply that they can transmit these traits to their progeny, and they could be used to develop synthetic populations (Apraku *et al*. 2013). Thus, the parent UON-2015-119 could be used to develop superior varieties through hybridization, backcrossing, and recurrent selection methods (Apraku *et al*., 2015).

The SCA shows the non additive component of the genetic variation and is due to dominance and epistatic gene effects and is non-fixable in nature. The non additive component is useful in heterosis breeding (Kiyyo and Kusolwa, 2017). The involvement of the F_1 generation allows estimation of genetic parameters and assessment of dominance in the polygenic systems. The SCA indicates importance of the joint action of the genes of parental forms. However, great variability regarding SCA effects is unfavorable because it increases the probability of obtaining hybrid progenies with an average value of that trait (Murtadha *et al*., 2016). The SCA helps to establish the heterotic patterns of inbred lines and to identify superior hybrids (Legesse *et al*., 2009). Populations with high GCA also reveal hybrids with high SCA suggesting the presence of alleles with non addictive effects which are accumulated through selection (Vacaro *et al*., 2002; Asea *et al*., 2012). When two unrelated parents are crossed, they produce single cross hybrids heterozygous at all loci and which is thought to be superior to the two parents. This is not always the case as shown by the fact that the parent UON-2015- 50 showed poor GCA for all the disease parameters. Also, the parent UON-2015-119 showed poor SCA effects despite the desirable GCA effect for all the disease parameters. This implies that any breeding method chosen should first accumulate favourable genes in homozygous state while breaking the linkage blocks (Solanki and Gupta, 2001). Also, the parents could be selected for different traits for further improvement. Elite parents for use in hybrid development require that one considers the SCA and the GCA (Makanda *et al*., 2010). From this study, the best crosses were derived from crosses which had low GCA values for the disease parameters. Thus, additive by epistatic and dominance by dominance gene interaction could be responsible for the resistance to the MLN. The non additive gene action which is also non allelic produces over-dominance which is non fixable in nature (Fasahat *et al*., 2016). Some crosses which showed high SCA effects, had only one good combiner implying that such combinations may have desirable transgressive segregations provided that the additive genetic system present in the crosses are acting in the same direction to reduce undesirable plant characteristics and maximize the characters in view which is important in breeding programs (Farag *et al*., 2012).

A parent good in *per se* performance may not necessarily produce better hybrids when used in hybridization. Concurrently, it also indicated that one parent of the worst combination could make the best combination if the other parent were selected properly. High SCA effects resulting from crosses where both parents are good general combiners (good GCA × good GCA) may be ascribed to additive × additive gene action. The high SCA effects derived from crosses including good × poor general combiner

parents may be attributed to favourable additive effects of the good general combiner parent and epistatic effects of poor general combiner, which fulfils the favourable plant attribute. High SCA effects manifested by low × low crosses may be due to dominance × dominance type of non-allelic gene interaction producing over dominance thus being non-fixable while in the presence of non-additive component, selection should be undertaken in later generations when these impacts are fixed in the homozygous lines (Fasahat *et al*., 2016).

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