

# Genetic analysis for resistance to *Sitophilus zeamais* (Motschulsky) among provitamin-A maize germplasm

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## Abstract

Maize biofortification is adopted as strategy to circumvent the high risk of vitamin A deficiency, accentuated by high incidence food losses due to storage insect pests in most developing countries where maize is an important staple crop. This study was initiated to understand the mode of inheritance for resistance to storage weevils among provitamin-A germplasm. A total of 72 provitamin-A maize testcross hybrids were evaluated for agronomic and adaptive traits in three sites, Namulonge, Serere and Ngetta in Uganda during the main season of 2015. Based on genotype x environment analysis of field traits, resultant grain from two divergent environments (Namulonge and Serere) were screened for resistance against *Sitophilus zeamais* in a no-choice laboratory. Line by tester analysis of combining ability indicated that both additive and non-additive gene effects were important in controlling the resistance parameters, including adult mortality, F1 insects which emerged, Median Development Period, Index of Susceptibility and Grain damage. Two provitamin-A inbred lines, CLHP0014 and CLHP0005 showed high GCA effects for reduced infestation with storage weevil. Broad sense heritability was moderate ( $0.19 \leq H^2 \leq 0.59$ ) and Narrow sense heritability ( $h^2$ ) was low ranging from 0.19 to 0.24. The two inbred lines with desirable GCA effect for weevil resistance could be used in the development of resistant breeding population. However, the low heritability of the trait observed, suggested that effective breeding methods be deployed to increase resistance to storage weevil, concurrently with research efforts to develop high nutritional quality maize varieties.

**KeyWords** provitamin-A maize, storage weevils, combining ability, heritability

## Introduction

Maize (*Zea mays* L.) is one of the target crops for micronutrients enhancement, especially the provitamin-A carotenoids in the world (Wurtzel et al., 2012). It is a staple food crop to much of the population of the developing countries where vitamin A deficiency (VAD) a severe public health concern (Hardjes et al., 2008; WHES, 2015). In Uganda, maize is the third most important food crop after banana and cassava, and accounts for 11% of daily caloric intake of the population (Hagglblade and Dewina, 2010); but VAD is still been reported as a national health problem (UBOS and ICF International Inc, 2012). A continuous production and consumption of maize with low level of vitamin A is one way of aggravating the VAD status in the country. The introduction of high provitamin-A maize varieties in the national cropping system would therefore help in alleviating the high incidence of VAD. However, maize is one of the agricultural food commodities highly susceptible to infestation by storage weevils (*Sitophilus zeamais*) which cause huge loss of nutrients and economic value of grain (Ajayi and Soyelu, 2013; Derera et al., 2014).

Maize weevils are economically important field-to-store pests of maize causing 30 to 80% grain weight loss in many tropical countries (Ajayi and Soyelu, 2013). Qualitative loss arises primarily from the alteration of the physical appearance and chemical constituents of the grains and leads to detectable reductions in vital nutrients such as sugar, proteins, lipids, minerals, vitamins, and other chemical constituents (Danjumma et al., 2009). It is, therefore, vital to develop varieties that combine high provitamin-A content with Host plant resistance as long term and cost-effective measure to reduce storage pest damage, which is an important factor in curbing post-harvest loss (Mwololo et al., 2012). Developing quality nutritional and weevil resistant maize varieties requires information about the inheritance of the traits and the amount of genetic variation among the available germplasm. Such information will guide the choice of breeding method and the type population to need to achieve the goal. An analysis of combining ability for resistance to storage weevils among provitamin-A maize germplasm, would help in selecting good parents and best cross combinations for much gain in

the breeding program. Studies focused on the inheritance of resistance to maize weevils have reported the importance of both additive and non-additive gene effects (Derera et al., 2014; Dari et al., 2010; Kim and Kossou, 2003; Derera et al., 2001a). Nevertheless, the maize genotypes used in most of these studies are predominantly of white grain colour, hence the need to extend related studies to provitamin-A maize genotypes. Additionally, the few studies conducted on inheritance for resistance against *S. zeamais* in Uganda have also been conducted on white maize germplasm (Kasozi et al., 2016; Gafishi et al., 2012), and to date there is no provitamin-A maize lines identified as good combiners for weevil resistance. These studies are required to generate valuable knowledge to maize breeders to select good genetic material using appropriate breeding methods to develop insect resistant provitamin-A maize varieties adapted to the Ugandan agro-ecologies. The key objective of this study, therefore was to determine the patterns of inheritance of resistance to *S. zeamais* among provitamin-A maize germplasm.

## Materials and Methods

### Genetic materials

A total of 72 provitamin-A maize testcross hybrids which were reported to have varying level of resistance

**Table 1. List of the 24 provitamin-A inbred lines used to develop the hybrids in 2014**

Nº	Genotype	Types	Origin
1	CML304	Line	CIMMYT
2	CML486	Line	CIMMYT
3	CML451	Line	CIMMYT
4	CLHP00306	Line	CIMMYT
5	CLHP00478	Line	CIMMYT
6	CLHP00476	Line	CIMMYT
7	CLHP0310	Line	CIMMYT
8	CLHP0290	Line	CIMMYT
9	CLHP00308	Line	CIMMYT
10	CLHP0302	Line	CIMMYT
11	CLHP0352	Line	CIMMYT
12	CLHP00294	Line	CIMMYT
13	CLHP00328	Line	CIMMYT
14	CLHP0301	Line	CIMMYT
15	CLHP0331	Line	CIMMYT
16	CLHP0289	Line	CIMMYT
17	CLHP00434	Line	CIMMYT
18	CLHP0014	Line	CIMMYT
19	CLHP0002	Line	CIMMYT
20	CLHP0006	Line	CIMMYT
21	CML300	Tester	CIMMYT
22	CLHP0005	Tester	CIMMYT
23	CLHP0003	Tester	CIMMYT
24	CLHP0020	Tester	CIMMYT

to *S. zeamais* were used in the experiment (Sodedji et al., 2016). These were single cross hybrids developed using a Line by tester mating design of four lines used as testers (males) crossed to 20 other lines (females) in September to December 2014, at the National Crops Resources Research Institute (NaCRRI), Namulonge in Uganda (Table 1). Testcross hybrids were evaluated in the main cropping season of 2015 (April to August) in three contrasting environments in Uganda-NaCRRI, National Semi-Arid Resources Research Institute (NaSARRI) in Serere, and Ngetta Zonal Agricultural Research and development Institute (Ngetta-ZARDI). Concurrently, seeds of the testcrosses (F1s) were self-pollinated at two divergent environments (Namulonge and Serere) in Uganda in 2015 (April to August) to produce F2 grains which were screened against *S. zeamais* at the entomology laboratory unit of NaCRRI-Uganda from September to December 2015. The F2 grains are the generation normally stored by farmers and therefore the most vulnerable to weevils damage (Siwale et al., 2009).

### Laboratory screening of provitamin-A maize genotypes for resistance to maize weevil (*Sitophilus zeamais*)

Screening for evaluating the resistance level of the hybrids provitamin-A maize genotypes against the maize weevil was done following the procedure used by Sodedji et al. (2016). This involved obtaining four subsamples (replicates) of 50 grams seeds of each maize genotype, wrapped in a polythene bag and then frozen it at -20 °C for 2 weeks to kill any insect/egg that could have attacked the grains in the field described by Siwale et al. (2009). After this operation, each seed sample was transferred to 250 cm<sup>3</sup> evaluation jar and a total of 32 unsexed insects reared under laboratory conditions was used to infest the maize kernels in each glass jar. The jars were laid in Alpha Lattice Design. Samples were given 10-days oviposition period after which all adult insects, dead and living were removed and counted. After 25 days of incubation (Gwinner et al., 1996; Derera et al., 2001a) F1 progeny insects were counted and removed from the jars at 2 days interval until no more insect emerged from the jars (Dhliwayo et al., 2005). The parameters measured included:

- Median Development Period (MDP) computed as the number of days from the middle period of oviposition (5 days) to the middle emergence of progeny,
- Index of Susceptibility (IS): calculated using the

method proposed by Dobie (1977). This involves the number of F1 progeny of weevils which emerged from each jar and the median development period:

$$(IS) = \frac{\log_e (\text{total of F1 progeny emerged})}{\text{Median development period}} \times 100$$

iii. Grain damage expressed as percentage of holed grains in a sample of 100 grains randomly sampled each individual jars.

iv. Number of F1 insects emerged, computed as the cumulative number of F1 insects progeny insects counted and removed from the jars at every 2 days interval until.

### Data analysis

Determination of the magnitude of genetic variation and the mode of inheritance, were done by analyzing the four parameters of weevil resistance using GenStat (VSN International, 2012). Estimation of combining ability of parental lines and heritability were considered in determining the inheritance patterns of the resistance to storage weevils. This allowed quantifying the magnitude of the additive and non-additive gene action for weevil resistance among provitamin-A maize germplasm. Restricted Maximum Likelihood was used to determine and analyze the variance of the crosses. Female and male parents were considered as fixed factors whereas locations were random using the following linear model:

$Y_{ijk} = \mu + m_i + f_j + s_{ij} + l_k + ml_{ik} + fl_{jk} + sl_{ijk} + e_{ijk}$ . Where  $Y_{ijk}$  = observed value from each experimental unit,  $\mu$  = grand mean,  $l_k$  = effect of the  $k^{\text{th}}$  location,  $m_i$  = GCA effect of the  $i^{\text{th}}$  male parent,  $f_j$  = GCA effect of  $j^{\text{th}}$  female parent,  $s_{ij}$  = SCA effect of the  $i^{\text{th}}$  male and the  $j^{\text{th}}$  female parents,  $ml_{ik}$  = interaction effect of  $i^{\text{th}}$  male parent GCA by the  $k^{\text{th}}$  location,  $fl_{jk}$  = interaction effect of  $j^{\text{th}}$  female parent GCA by the  $k^{\text{th}}$  location,  $sl_{ijk}$  = interaction effect of the  $i^{\text{th}}$  male and the  $j^{\text{th}}$  female parents SCA by the  $k^{\text{th}}$  location and  $e_{ijk}$  is the experimental error.

Components of genotypic variances were deter-

mined using the procedure presented in the skeleton ANOVA table (Table 2). General Combining Ability (GCA) effect was estimated for a given parental line as the difference between the mean of all crosses involving that parent and the grand mean. The Specific Combining Ability (SCA) of a particular cross was computed as the difference between the observed mean performance of the cross and its predicted mean. GCA and SCA effects were tested by a two-sided t-test to determine if they significantly differed from 0, based on the standard error associated with the estimate of that effect.

As defined by Sprague and Tatum (1942), general combining ability (GCA) is a measure of additive genetic effects while specific combining ability (SCA) is related to the non-additive genetic effects. Therefore, the relative importance of the additive gene effects in determining progeny performance was assessed by estimating the components of variance and expressing them in the ratio calculated as  $\sigma^2_{GCAm} + \sigma^2_{GCAF}/(\sigma^2_{GCAm} + \sigma^2_{GCAF} + \sigma^2_{SCA})$ , (Baker, 1978). The closer this ratio is to unity, the greater the predictability based on general combining ability alone (Baker, 1978). The analogous broad-sense ( $H^2$ ) and narrow-sense ( $h^2$ ) heritability were estimated on genotype means basis as follows (Dabholkar, 1999):

$$H^2 = \frac{\sigma^2_{GCAF} + \sigma^2_{GCAm} + \sigma^2_{SCA}}{\sigma^2_{GCAf} + \sigma^2_{GCAm} + \sigma^2_{SCA} + (\sigma^2_{l_{GCAm}}/l) + (\sigma^2_{l_{GCAF}}/l) + (\sigma^2_{l_{SCA}}/l) + (\sigma^2_e/b)}$$

$$h^2 = \frac{\sigma^2_{GCAF} + \sigma^2_{GCAm}}{\sigma^2_{GCAf} + \sigma^2_{GCAm} + \sigma^2_{SCA} + (\sigma^2_{l_{GCAm}}/l) + (\sigma^2_{l_{GCAF}}/l) + (\sigma^2_{l_{SCA}}/l) + (\sigma^2_e/b)}$$

**Table 2. Skeleton ANOVA for the line by tester across locations**

Source	D-f	MS	Expected Mean of Square	F - denominator
Locations (Loc)	l-1	---		M7
Lines (GCAF)	f-1	M1	$\sigma_e^2 + m\sigma_{lf}^2 + ml\sigma_{f}^2$	M3
Testers (GCAm)	m-1	M2	$\sigma_e^2 + f\sigma_{lm}^2 + lf\sigma_m^2$	M4
Lines x Loc	(l-1) (f-1)	M3	$\sigma_e^2 + m\sigma_{lf}^2$	M7
Testers x Loc	(l-1) (m-1)	M4	$\sigma_e^2 + f\sigma_{lm}^2$	M7
Lines x Testers (SCA)	(f-1) (m-1)	M5	$\sigma_e^2 + r\sigma_{lmf}^2 + l\sigma_{mf}^2$	M6
Line x Testers x Loc	(l-1) (m-1) (f-1)	M6	$\sigma_e^2 + r\sigma_{lmf}^2$	M7
Pooled Error	l (mf-1)	M7	$\sigma_e^2$	

Df= degree of freedom, MS=Mean of Square; Loc= location f=females, m = males,  $\sigma_m^2 = \sigma_{GCAm}^2$ ;  $\sigma_f^2 = \sigma_{GCAF}^2$ ;  $\sigma_{fm}^2 = \sigma_{l_{GCAm}}^2$ ;  $\sigma_{lf}^2 = \sigma_{l_{GCAF}}^2$ ;  $\sigma_{lmf}^2 = \sigma_{l_{GCAm}}^2 \times SCA$ ; GCAF = General combining ability of the female parents; GCAm = General combining ability of the male parents.

**Table 3. Analysis of variance of combining ability effects for five grain susceptibility parameters across locations**

Source	Df	Adult Mortality	F1 Insects emerged	MDP	GD	IS
Loc.	1	648.66***	8525.8***	3277.1***	6179.1***	201.79***
Line (GCAf)	19	96.19***	692.2*	2.33	301.6**	1.77***
Tester (GCAm)	3	88.95*	1106.3*	32.36*	639.1	5.06*
Loc. x Line	19	1.89	258***	6.54***	88.8***	1.11***
Loc. x Tester	3	4.97	86.4	1.23	103.9***	0.32
Line x Tester (SCA)	49	86.15*	453.4***	5.47	181.2***	1.27*
Loc.x Line x Testers	49	46.82***	232.3***	5.47***	137.1***	0.76***
Pooled error		11.02	48.42	1.44	19.22	0.18
Pooled error Df	424		444	430	412	444

Loc = Location, GCAf = General combining ability of the female parents, GCAm = General combining ability of the male parents, SCA= specific combining ability. Adult Mortality= percentage of dead insects after 10 days of oviposition; MDP=Median Development Period, IS= Index of susceptibility, GD= Grain damage. \*\*\*Significant at P<0.001, \*\*Significant at P<0.01, \*Significant at P<0.05.

## Results

### Combing ability of the provitamin-A maize lines for resistance to *Sitophilus zeamais*

Line by Tester analysis of combining ability revealed significant differences in the general combining ability effects of both tester (Male parents) and line (Female parents) for all the grain resistance parameters assessed, except Median Development period and grain damage for lines and testers, respectively (Table 3). Male parents showed large differences in general combining ability (GCAm) for F1 insects emerged (P < 0.05), median development period (MDP) (P < 0.001) and index of susceptibility (IS) while large differences for adult mortality was observed in the general combining ability effects of the female parents (GCAf). There was significant difference in the specific combining ability effects (SCA) of the crosses for all parameters assessed (Table 3). Location x Line was significant for all parameters except Adult Mortality. On the other hand, the interaction between location and Tester significantly varied for Median Development Period (MDP) and Grain Damage (GD). Location x Line x Tester was significant for all parameters assessed (Table 3).

### General and Specific combining abilities effects for resistance to *Sitophilus zeamais* among the provitamin-A maize germplasm

Significant GCA effects were observed among the provitamin-A maize germplasm for the grain resistance parameters assessed (Table 4). Two inbred lines CML304 (-5.45\*) and CLHP00478 (-5.80\*\*) contributed to low mortality of adult insects as shown by their large negative GCA effects while Inbred line CLHP0002 (9.38\*\*\*) showed a high desirable GCA effect for increased mortality of adult insects. Three

lines; CML486, CLHP00294, CLHP00331 and the tester CML300 had significantly contributed to an increase number of weevils in the hybrid progenies as shown by their large significant and positive GCA effects. On the other hand, the lines CLHP00306, CLHP0290, CLHP0289, CLHP0014, CLHP0002, and CLHP0005 had exhibited a significant negative GCA effects for F1 insects emerged. GCA effects for Median Development Period (MDP) was significant and positive for the tester CLHP0005 (1.22\*\*) while the tester CML300 (-1.11\*\*\*) had significantly contributed to a reduction of the median development period. Significant GCA effects for low Grain Damage (GD) was observed in the lines CLHP00306, CLHP0289, CLHP0014; CLHP0002 and the tester CLHP0020 unlike two of the lines (CLHP0310 and CLHP0006) and two testers (CML300, CLHP0003) exhibited high GCA effects for increased grain damage (Table 4). Overall, the highest negative GCA effect for Index of Susceptibility (IS) was observed in inbred line CLHP0014 (-1.08\*\*). The tester CLHP0005 (-0.42\*) and the line CLHP00306 (-0.62 \*) had also significantly contributed to a lower index of susceptibility values. The line CLHP00294 showed a positive GCA effects for index of susceptibility (0.92\*).

Table 5 presents the specific combining ability (SCA) for grain resistance parameters in some provitamin-A maize crosses evaluated across environments. Averaged over environments, the crosses CML486/ CLHP0005 and CLHP00308/CML300 had a significant SCA effects for low number of F1 insects emerged and low percentage of grain damage. Opposite responses were obtained for these two parameters in the cross combinations CML486/CML300, CLHP00308/ CLHP0020 and CLHP00434/CLHP0005. GCA effects for Adult Mortality were significant and positive in the crosses CLHP0290/CLHP0020 and CLHP00434/

**Table 4. General combining ability effects of the 24 provitamin-A parental lines for the five grain resistance parameters assessed across two locations (Namulonge and Serere) in 2015**

Genotypes	Adult Mortality	F1 Insects emerged	MDP	GD	IS
<b>Lines</b>					
CML304	-5.45*	4.91	1.22	2.35	0.05
CML486	-0.81	10.81*	0.41	7.11	0.21
CML451	-2.31	5.01	-0.76	3.89	0.43
CLHP00306	1.89	-9.89*	0.74	-7.84*	-0.62*
CLHP00478	-5.80**	1.31	0.37	-0.11	-0.13
CLHP00476	-0.31	-2.79	0.37	-2.84	-0.24
CLHP0310	-3.12	8.91	-0.12	14.13*	0.52
CLHP0290	3.87	-10.99*	0.23	-5.82	-0.44
CLHP00308	3.90	1.11	-0.87	2.56	0.28
CLHP0302	2.22	2.41	-0.70	3.46	0.35
CLHP0352	1.04	2.51	-0.27	1.42	0.21
CLHP00294	3.40	18.51***	-0.76	5.38	0.92*
CLHP00328	-2.14	-5.39	-0.29	-3.57	0.00
CLHP0301	-2.31	-2.09	0.67	-3.72	-0.21
CLHP00331	0.18	14.51*	0.19	5.39	0.57
CLHP0289	-3.07	-14.79*	-0.61	-7.28*	-0.57
CLHP00434	-4.01	-5.79	0.16	-5.19	-0.16
CLHP0014	3.65	-15.19*	0.09	-8.22*	-1.08**
CLHP0002	9.38***	-11.99*	-0.12	-11.09*	-0.47
CLHP0006	0.15	0.91	-0.01	9.13*	0.01
<b>Testers</b>					
CML300	-0.50	8.22***	-1.11**	4.98***	0.48
CLHP0005	-1.77	-4.98*	1.21***	-2.52	-0.42**
CLHP0003	0.41	1.86	-0.32	3.05*	0.19
CLHP0020	1.87	-3.01	-0.10	-4.18**	-0.12

Adult Mortality= percentage of dead insects after 10 days of oviposition; MDP=Median Development Period, GD= Grain damage and IS= Index of susceptibility \*\*\*Significant at P<0.001, \*\*Significant at P<0.01, \*Significant at P<0.05.

CLHP0020 while CLHP0290/CML300 and CLHP00434/CLHP0005 showed negative GCA effects for that parameter. The hybrid CML486/CLHP0020 had a large SCA effect for a low number of F1 insects emerged but its SCA effect was not significant for grain damage even though a negative effect was observed. CML451/CLHP0005 showed a significant positive SCA effects for grain damage while the cross between CML451 and CLHP0003 had a negative and significant SCA effect. CLHP0301/CLHP0005 showed a significant and large positive specific combining ability for grain damage. The crosses CLHP00434/CLHP0005 and CLHP0002/CML300 showed a positive SCA effects for a high index of susceptibility. None of the cross combinations had a desirable significant SCA effect for Median Development Period (MDP) (Table 5).

#### **Baker's ratio and heritability estimates for resistance to *Sitophilus zeamais* among the provitamin-A maize germplasm**

Components of variance were estimated and expressed in ratio as shown in Table 6, in order to determine the type of gene action involved in the variation observed in the progenies performance for the traits under study as recommended by Baker (1978). For the five grain resistance parameters assessed, median development period (MDP) and grain damage (GD) had a Baker's ratio higher than 0.5 (Table 6). The Baker's ratio values for Adult Mortality, F1 insects emerged and Index of Susceptibility (IS) were lower than 0.5 ( $0.4 \leq$  Baker's ratio  $< 0.5$ ). The estimation of heritability values for resistance to maize weevils among the studied provitamin-A maize germplasm is presented in Table 6. Broad sense heritability ( $H^2$ ) values were moderate

**Table 5. Specific combining ability effects for grain resistance parameters in selected provitamin-A maize hybrids**

Hybrids	Adult Mortality	F1 insects emerged	MDP	GD	IS
CML486/CML300	-3.81	34.80***	-1.21	17.58**	1.39
CML486/CLHP0005	6.64	-30.50**	0.24	-17.24**	-1.39
CML486/CLHP0020	-2.08	-22.22*	2.80	-10.85	-1.16
CML451/CLHP0005	-2.29	17.13	-1.01	21.71***	0.85
CML451/CLHP0003	-3.96	-19.21	1.98	-13.22**	-1.01
CLHP0290/CML300	-14.18***	-10.00	2.17	-4.76	-0.88
CLHP0290/CLHP0020	10.25***	17.97	-1.38	10.72	1.17
CLHP0308/CML300	-3.54	-21.56*	-0.54	-12.54*	-0.75
CLHP0308/CLHP0020	-4.82	22.79*	-0.39	17.28*	0.93
CLHP0301/CLHP0003	-2.92	16.16	0.94	14.68*	0.26
CLHP00434/CLHP0005	-10.06*	25.40*	-0.53	14.21*	1.59**
CLHP00434/CLHP0020	15.12**	-11.08	-0.25	-3.77	-0.87
CLHP0002/CML300	-7.54	17.83	-2.60	17.02*	1.37*

Adult Mortality= percentage of dead insects after 10 days of oviposition; MDP=Median Development Period, GD= Grain damage and IS= Index of susceptibility

\*\*\*Significant at  $P<0.001$ , \*\*Significant at  $P<0.01$ , \*Significant at  $P<0.05$ .

**Table 6. Variance components, Baker's ratio, Broad sense and Narrow sense heritability for grain resistance parameters across locations**

Variance components	Adult Mortality	Grain resistance parameters			
		F1 Insects emerged	MDP	GD	IS
$\sigma^2_{GCA_f}$	2.95	13.57	-0.13	6.65	0.02
$\sigma^2_{GCA_m}$	0.52	6.37	0.19	3.34	0.03
$\sigma^2_{SCA}$	4.91	27.64	-0.0002	5.5	0.06
$\sigma^2_{Loc \times GCA_f}$	-0.6	13.09	0.32	4.34	0.05
$\sigma^2_{Loc \times GCA_m}$	-0.08	0.47	-0.002	1.02	0.002
$\sigma^2_{Loc \times SCA}$	8.95	45.96	1.01	29.46	0.14
$\sigma^2_e$	11.03	48.42	1.44	19.22	0.18
<b>Baker's Ratio</b>	0.41	0.42	1	0.64	0.44
<b>H<sup>2</sup></b>	0.59	0.57	0.19	0.43	0.48
<b>h<sup>2</sup></b>	0.24	0.24	0.19	0.28	0.21

Loc= Location, GCA<sub>f</sub> = General combining ability of the female parents, GCA<sub>m</sub> = General combining ability of the male parents, SCA= specific combining ability. Adult Mortality= percentage of dead insects after 10 days of oviposition; MDP=Median Developmental Period, IS= Index of susceptibility. H<sup>2</sup> = broad-sense heritability and h<sup>2</sup> = narrow-sense heritability.

for all parameters ( $0.59 \leq H^2 \leq 0.43$ ) except for the MDP where a low value was obtained whilst narrow sense heritability ( $h^2$ ) values were low ranging from 0.19 to 0.28.

## Discussion

Mechanisms of resistance to *S. zeamais* vary among maize germplasm and resistance should not be based on a single trait alone (Mwololo et al., 2013). In the present study, we based our analysis on five traits, including median developmental period of weevils, the percentage of damaged grain due to weevil infestation, the total number of insects progenies and the Index of susceptibility which have been used in several

research on resistance to *S. zeamais* to discriminate among maize genotypes (Dobie 1977; Siwale et al. 2009; Dhliwayo et al., 2005; Tefera et al., 2011; Mwololo et al., 2013). Results revealed significant variation in the general combining ability and specific combining ability effects for all the traits assessed, indicating that both additive and non-additive genetic effects are involved in the transmission of resistance to *S. zeamais* among the provitamin-A maize germplasm. Similar results have been reported in previous studies (Kang et al., 1995; Dhliwayo et al., 2005; Gafishi et al., 2012). Although, the two gene actions are involved in the inheritance of resistance to maize weevils, the magnitude of their contribution differed. In the present

study only median development period (MDP) and grain damage (GD) had a Baker's ratio greater than 0.5, while for the other three parameters the ratio was lower than 0.5 (approximately 0.4). This implies that the additive genetic effects were relatively more important in determining the performance of the provitamin-A hybrids maize for the median development and grain damage whilst the non-additive genetic effects were relatively more important for adult mortality, F1 insects emerged and index of susceptibility. These results suggested that, considering this set of testcrosses, the performance of the hybrids provitamin-A maize genotypes for weevils resistance cannot be accurately predicted based on the general combining ability effects of their parents alone. In estimating the magnitude of additive and non-additive genetic effects in the inheritance of resistance to maize weevils in F2 maize grains, Dhliwayo et al. (2005) found that the variance due to SCA effects was more important than the GCA effects for F1 insects emerged. However, other studies pointed out that the additive genetic effects are more important in predicting the performance of the progenies for weevil resistance (Kang et al., 1995; Derera et al., 2001b; Kim and Kossou, 2003). Some of the parental lines of the provitamin-A maize hybrids showed a good GCA effects for resistance. The line CLHP0014 and the tester CLHP0005 which were previously reported as moderately resistant lines (Sodedji et al., 2016), had desirable GCA effects for low number of F1 insects and index of susceptibility. CLHP0014 had a good combining ability for increasing the median development period of the insects in the hybrids while the tester CLHP0005 combines well for low grain damage. These genotypes are promising provitamin-A inbred lines that can be used for population improvement.

Important contribution of the specific combining ability (SCA) in the responses of the hybrids provitamin-A maize against *S. zeamais* was observed. This is clearly demonstrated in some of the crosses. CML486/CLHP0005 and CLHP00308/CML300 were the good cross combinations for low number of insects emerged and low percent of grain damage. CML486/CLHP0020 had also showed a desirable SCA effect for a low number of F1 insects emerged while a good SCA effect for grain damage was obtained from the cross between the line CML451 and the tester CLHP0003. The crosses CLHP00434/CLHP0005 and CLHP0002/CML300 showed a positive SCA effects for a high index of susceptibility.

Both GCA and SCA effects were highly influenced by environment and this combined with the large effect of the variance due to the specific combining ability

resulted in low narrow sense heritability estimates obtained for the grain resistance parameters (Table 3 and Table 6). Dhliwayo et al., (2005) reported that heritability of resistance to maize weevils is likely to be low to moderate because of the significant variance induced by the non additive gene effects. The low heritability values obtained in the present study indicates the low transmissibility of the performance of the provitamin-A maize lines to their progenies (Hallauer et al., 1988), and this would slow progress in moving resistance into elite lines (Bervigson, 2001). However, combining conventional breeding approach with available molecular tools at the very early generation of the breeding process may quicken the genetic gain in breeding for this trait.

## Conclusions

This study identified provitamin-A maize lines with good combining ability for weevil resistance that could be used in breeding for improved resistance to storage weevils among provitamin-A maize varieties. Low narrow sense heritability and Baker's ratio estimates were obtained for the major maize weevil resistance parameters assessed, suggesting that selection for weevil resistance would be less effective at early generation of breeding.

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