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Full Length Research Paper

Genetic inheritance of resistance to *Fusarium redolens* in cowpea

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Fusarium **related root rots have been associated with reduced cowpea productivity in Uganda. Sources of genetic resistance to *Fusarium redolens* which was found to be the most virulent have been identified but the mode of inheritance of the genes conferring the resistance is unknown. This study aims to investigate how the genes for resistance to *F. redolens* are inherited in cowpea. Four *F. redolens* root rot resistant cowpea genotypes were crossed with four intermediately resistant and 2 susceptible cowpea genotypes using North Carolina mating design II. The F_1 and the parents were evaluated and data were collected on resistance to seed rot, leaf chlorophyll amount, produced lateral roots, response to plant mortality and root rot severity. Results revealed that additive gene effects were significant for all evaluated traits and non-additive genetic effects were significant in resistance to seed rot and chlorophyll amount. General combining ability (GCA) effects showed that the Asontem genotype was a good combiner for increased lateral roots production and resistance to root rot. Degree of dominance estimates revealed that response to plant mortality, root rots and increased lateral root production traits were recessively inherited while seed rot and amount of leaf chlorophyll were dominantly inherited.**

Key words: *Vigna unguiculata,* Baker's ratio, combining ability, *Fusarium redolens,* heritability, Uganda.

INTRODUCTION

Cowpea [*Vigna unguiculata* (L.) Walp.] which originated in Africa (Tan et al., 2012) is one of the most important grain legume crop grown in sub-Saharan Africa (Badiane et al., 2012). Amongst its important attributes, cowpea can be used in human nutrition where it provides adequate amount and quality of protein and as animal feed (hay) during the dry season in many parts of Africa (Badiane et al., 2012). It has high protein content ranging between 23 and 32% of seed weight rich in lysine and tryptophan, and a considerable amount of vitamins (folic

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Table 1. Characteristics of the used parents.

Variety	Resistance status to *F. redolens*	Origin
Asontem	Resistant	Ghana
IT89KD-288	Resistant	Nigeria
NE 70	Resistant	Uganda (landrace)
Dan1la	Resistant	Nigeria
NE 50	Intermediately resistant	Uganda (landrace)
NE 6	Intermediately resistant	Uganda (landrace)
SECOW 2W	Intermediately resistant	Uganda (cultivar)
SECOW 3B	Intermediately resistant	Uganda (cultivar)
KVU 27-1	Susceptible	Uganda (landrace)
WC 66	Susceptible	Uganda (landrace)

acid and vitamin B) attributes that have led to the crop being referred to as the "poor man's meat" (Tan et al., 2012). Additionally, cowpea is an important source of income to the resource poor for farmers in Africa (Langyintuo et al., 2003; Timko et al., 2007; Timko and Singh, 2008; Diouf, 2011). Moreover, cowpea is an important rotation and cover crop with nitrogen-fixing ability which makes its valuable when rotated with cereal crops (Timko et al., 2007).

In Uganda, cowpea is intensively grown in the eastern and northern regions with over 90% of the households engaged in commercial production for food and cash income. Although, the expected yield potential of cowpea attained on station is 3,000 kg/ha, yield at farmer's level averages at 500 kg/ha (Rusoke and Rubaiyaho, 1994). The low productivity has been attributed to several factors, but most importantly is due to prevalence of diseases (Rusoke and Rubaiyaho, 1994; Edema et al., 1997). Among the diseases, *Fusarium* root rot (*Fusarium redolens*) has been reported to be devastative to cowpea in Uganda. The disease can result in extremely high infection especially with susceptible cowpea cultivars, when prevailing environmental and host factors are favourable.

Development and use of resistant varieties is the most sustainable and cost effective method in the management of various diseases (Pottorff et al., 2012). Moreover, the information on inheritance of resistance to *F. redolens* is imperative for future breeding activity to develop resistant cowpea varieties. However, the mode of gene action and the pattern of inheritance of resistance to *Fusarium* root rots of cowpea in Uganda have not been well understood. Therefore, the use of sources of resistance to introgress resistance into susceptible landraces with desired agronomic traits in breeding programmes is limited. The estimates of combining ability and gene actions are important in identifying parents with superior genes based on the general combining ability and specific combining ability effects with better mean performance. This information could be used as a basis of determining the breeding method and the population to use in order to reach target goal. Therefore, the objective of this study was to determine the mode of inheritance governing resistance to *F. redolens* in cowpea in Uganda.

MATERIALS AND METHODS

Study area

The study was conducted in a screen house at Makerere University Agricultural Research Institute, Kabanyolo (MUARIK). MUARIK is located between 320 37'E, and 00 28'N at 1200 m above sea level in Wakiso district, Central Uganda. The annual rainfall and temperature were 1150 mm and 21.50°C, respectively. The experiment was conducted from May to September, 2016.

Hybridization

Ten cowpea parental lines were selected for this study based on their reaction to root rot caused by *F. redolens*. The selected resistant cowpea genotypes (males: ASONTEM, IT98KD-288, Dan 1LA and NE 70) were crossed with landraces and cultivars that had intermediate resistance (female: NE 50, NE 6, SECOW 2W and SECOW 3B) and susceptibility (females: KVU 27-1 and WC66) (Table 1) using North Carolina Mating Design II (NCII). The parents were planted in the crossing block in the screen house constituting one row of twenty-six plants (13 hills) at 20 × 100 cm spacing. Five grams of di-ammonium phosphate was used per hill of 2 plants to boost the growth of the plants. At 35 days after planting (DAP), the plants were staked to avoid intertwining with different genotypes. In NCII, every progeny family has half sib relationships through both common male and female. This was accomplished by mating n_1 male with n_2 female in all possible combinations to give n_1n_2 progeny families (Nduwumuremyi et al., 2013). Crossing was done to generate 24 F_1 family crosses. At maturity, the seeds of each F_1 cross were harvested separately.

Evaluation of F_1 crosses and parents for resistance to *Fusarium* root rot in screen house

Sterile sorghum was used as a medium to multiply the inoculum as described by Mugisha (2010). *F. redolens* was cultured for 3 weeks in 500-ml capacity flasks each containing 200 g of sorghum seeds.

Two flasks of mature *F. redolens* were added in each of the six wooden trays (150 cm× 100 cm× 13 cm) containing thoroughly mixed pre-sterilized soil (3:1, loam: sand) (Mukankusi et al., 2011). The trays were covered with dark polythene for a week to incubate the inoculum in the soil. Three susceptible cowpea genotypes, IT889, KVU 27-1 and WC 66, were then planted in each of the trays for up to 28 days and uprooted. This was repeated 3 times to ensure that the trays had adequate inoculum. The trays were watered 4 days per week (Mugisha, 2010; Ongom et al., 2012). After each cycle, soil was removed from the trays and mixed thoroughly and then redistributed equally to encourage uniform inoculum amounts before the test lines were planted. Planting was done using alpha lattice design (5 blocks × 7 plots) with 6 replications. The seeds of F_1 cross and parents were surface sterilized and planted separately in the *F. redolens* inoculated soil contained in 6 wooden trays. Each plot consisted of a single row of 7 plants representing a particular material (F_1 cross or parent). The trays were placed on raised benches in the screen house and watered four times a week (Mugisha, 2010).

Data collection

Seed rot was assessed by counting the number of germinated seeds for all the test populations 6 days after planting (DAP) and expressing the number as a proportion of the total seeds planted (Equation 1). Leaf chlorophyll content was assessed 27 DAP using PhotosynQ; Soil Plant Analysis Development 3 (SPAD 3). On the 28th day, response to plant mortality was assessed by counting the number of dead plants per test population and recorded as a percentage of dead plants (Equation 2). Thereafter, the remaining plants per line (cross or parent) were carefully and separately uprooted and then the below ground parts of the plant (roots and hypocotyls) were washed under running tap water. The percentage of plants per line with lateral roots above or at the ground level was recorded (Equation 3), and root rot severity was assessed by scoring root and hypocotyl damage according to the C1AT 1-9 scale (Abawi and Pastor-Corrales, 1990), where 1=No visible symptoms, 3=Light discoloration either without necrotic lesions or with approximately 10% of the hypocotyl and root tissues covered with lesions, 5=Approximately 25% of the hypocotyl and root tissues covered with lesions, but tissues remain firm with deterioration of the root system, 7=Approximately 50% of the hypocotyl and root tissues covered with lesions combined with considerable softening, rotting, and reduction of root system, 9=Approximately 75% or more of the hypocotyl and root tissues affected with advanced stages of rotting combined with severe reduction in the root system and dead plants.

% Germination = Number of germinated seed / Total planted × 100 (1)

% Dead plants = Counted dead plants / Total emerged plants × 100 (2)

% Lateral roots = Number of plants with lateral roots/ Total scored plants × 100 (3)

Data analysis

Determination of combining ability effects

Variance of the crosses (Equation 4) was analysed using GENSTAT 12th edition (Payne et al., 2009). Female and male parents were considered as fixed factors. General combining ability (GCA) effect was estimated as the difference between the grand mean and the mean of all crosses of a particular parent. High GCA effects indicated predominance of additive genes over the non-additive and vice versa. The specific combining ability (SCA) was estimated as the difference between the predicted mean of a particular cross and its observed mean. High SCA effects meant more none-additive gene effects (where dominance and/or epistasis may be prominent). A two-sided t-test was used to test and determine if individual GCA and SCA effects were significantly different from 0, based on the standard error associated with that effect.

$$y_{ijkl} = u + r_i + b/r_{ij} + g_k + g_l + s_{kl} + e_{ijkl} \quad (4)$$

where y_{ijkl} = observed value from each experimental unit, u = general mean, r_i = effect of the i^{th} replication, b/r_{ij} = effect of j^{th} block nested within k^{th} replication, g_k = GCA effect of the k^{th} female parent, g_l= GCA effect of the l^{th} male parent, s_{kl} = SCA effect of k^{th} male mated to the l^{th} female and e_{ijkl} = the environmental effect of $ijkl^{th}$ observation.

Determination of coefficients of genetic determination and Baker's ratio

Knowledge of heritability helps to guide plant breeders to predict behaviour of succeeding generation and response to selection (Falconer and Mackay, 1996). According to Fehr (1987) heritability is a ratio of genotypic variance ($\delta^2 g$) to phenotypic variance ($\delta^2 p$). There are 2 types of heritability, namely, narrow sense coefficient of genetic determination (NS-CGD) denoted by h^2 which estimates the additive genetic contribution to phenotypic variance (Equation 5), and the broad sense coefficient of genetic determination (BS-CGD) denoted by H which considers all the genetic contribution to phenotypic variance including additive and non-additive effects (Equation 6) (Falconer and Mackay, 1996). Both NS-CGD and BS-CGD approximates heritability for non-random samples therefore the results cannot be used to infer outside the purposely selected genotype. The ratio of GCA variance to SCA variance was also estimated according to Baker's ratio to determine the relative significance of additive versus non-additive effects (Baker, 1978) (Equation 7).

$$\text{NS-CGD } (h^2) = \frac{\sigma^2 GCA(R) + \sigma^2 GCA(s)}{\sigma^2 GCA(R) + \sigma^2 GCA(s) + \sigma^2 SCA + \sigma^2 e/r} \quad (5)$$

$$\text{BS-CGD } (H) = \frac{\sigma^2 GCA(R) + \sigma^2 GCA(s) + \sigma^2 SCA}{\sigma^2 GCA(R) + \sigma^2 GCA(s) + \sigma^2 SCA + \sigma^2 e/r)} \quad (6)$$

$$\text{Bakers ratio} = \frac{\sigma^2 GCA(R) + \sigma^2 GCA(s)}{\sigma^2 GCA(R) + \sigma^2 GCA(s) + \sigma^2 SCA} \quad (7)$$

Index of susceptibility

An index of susceptibility (IS) was developed based on the various evaluated parameters using Genstat 12^{th} edition through multiple regression of 4 variables with root rot severity as the response variate and percentage lateral roots, amount of chlorophyll and percentage of dead plants as the explanatory variates (Equation 8). This allowed establishment of a cumulative classification of the parents and their progeny based on the means of the traits they were evaluated for. Germination percentage was not included in this computation since it had earlier been observed to have no correlation to root rot severity.

$$\boldsymbol{IS} = \boldsymbol{constant} + \boldsymbol{LR}(\%) + \boldsymbol{DI}(\%) + \boldsymbol{CHL} + \boldsymbol{DP}(\%) \quad (8)$$

where IS = index of selection, LR = lateral roots, DI = disease incidence, CHL = chlorophyll, and DP = dead plants.

Table 2. Combing ability estimates, variance components, heritability and Baker's ratio for resistance of cowpea genotypes to F. redolens (genotype means basis).

Sources of variation	Degrees of freedom	Germination (%)	Chlorophyll amount	Dead plants (%)	Lateral roots (%)	Root rot severity
Replication	5	214.23***	4.60^{ns}	438.77***	331.55*	1.20***
Crosses	23	326.49***	8.42***	247.79***	350.57***	0.82***
GCA female	5	567.03***	9.81**	539.42***	539.64***	1.22***
GCA male	3	242.10***	11.38*	297.70*	824.71***	2.11***
SCA	15	263.19***	7.36**	140.59^{ns}	192.72^{ns}	0.43^{ns}
Error	134	37.37	2.94	81.92	117.50	0.26
Variance components						
σ^2 GCA male	-	34.12	1.41	35.96	117.87	0.31
σ^2 GCA female	-	132.42	1.72	114.38	105.53	0.24
σ^2 SCA	-	225.82	4.43	58.67	75.21	0.18
σ^2 error	-	37.37	2.94	81.92	117.50	0.26
Heritability						
h^2	-	0.39	0.30	0.52	0.54	0.56
H	-	0.91	0.72	0.72	0.72	0.74
Bakers ratio	-	0.42	0.41	0.72	0.75	0.75

*, **, ***: Significance at alpha 0.05, 0.01 and 0.001, respectively; ns: Not significant. h^2: Narrow sense heritability, H: Broad sense heritability, GCA: General combining ability; and SCA: Specific combining ability.

Estimation of degree of dominance for resistance to *F. redolens*

The average degree of dominance (d/a) for the resistant/susceptible crosses was determined according to Equation 9.

$$d/a = \frac{2*(F1-MP)}{\text{Resistant parent}-\text{susceptible parent}} \quad (9)$$

where d/a = degrees of dominance, F_1 = cross mean, MP = mean of two parents (P1 + P2)/2.

The results were interpreted as recommended by Kearsey and Pooni (1996), where $|d/a| = 1$ indicates complete dominance, $0 < |d/a| < 1$ indicates partial dominance, $|d/a| = 0$ indicates no dominance, and $|d/a| > 1$ indicates over-dominance.

RESULTS

Combing ability estimates, variance components, heritability and Baker's ratio for resistance of cowpea genotypes to *F. redolens*

The results of the combining ability analysis are shown in Table 2. The results indicated that the crosses had significantly different effects for all the traits studied ($p<0.001$). GCA effects of both female and male parents were also significantly different for all the parameters studied. As for the crosses' SCA effects, significant difference was observed only for percentage of germination and chlorophyll amount ($p<0.01$). Comparing the relative importance of additive genetic effects over non-additive effects, results showed that parameters, percentage of dead plants, lateral roots and root rot severity had high estimate Baker's ratio (BR>0.71), while percentage of germination and chlorophyll amount had a relatively moderate Baker's ratio (0.42 and 0.41, respectively). The estimate of broad sense coefficient of genetic determination was relatively high for all the parameters studied. On the other hand, the estimate of narrow sense coefficient of genetic determination was from relatively low for percentage of germination and chlorophyll amount (0.39 and 0.30, respectively) to moderate for percentage of dead plants and lateral roots and root rot severity ($0.51 < h^2 < 0.57$).

General combining ability (GCA) effects for resistance of parental genotypes to *F. redolens*

The two-sided t-student test (Table 3) showed that the parental lines Dan 1LA, SECOW 2W, and WC 66 had significant negative GCA effects ($P<0.01$, $P< 0.01$ and $P<0.05$, respectively) for germination percentage, while NE 50 and NE 6 had significant positive GCA effects for the same trait. Genotype WC 66 had the only negative and significant ($P<0.05$) GCA effect for amount of chlorophyll in the leaves. For percentage of dead plants due to *F. redolens* infection, genotype NE 6 had a negative and significant ($P<0.05$) GCA effect and WC 66 had a positive significant ($P< 0.05$) GCA effect. In the percentage of plants with lateral roots, ASONTEM had a significant ($P<0.05$) positive GCA effect, while NE 70 and WC 66 had negative and significant ($P<0.05$) GCA effect.

Table 3. General combining ability effects of cowpea genotypes for resistance to *F. redolens*.

Genotype	Germination (%)	Chlorophyll amount	Dead plants (%)	Lateral roots (%)	Root rot severity
Male parent					
ASONTEM	2.69^{ns}	1.46^{ns}	2.65^{ns}	14.93*	-0.86**
Dan 1LA	-9.42**	-0.03^{ns}	7.56^{ns}	-0.90^{ns}	0.41^{ns}
IT89KD-288	2.26^{ns}	0.41^{ns}	-9.14^{ns}	-0.30^{ns}	0.09^{ns}
NE 70	4.47	-1.84^{ns}	-1.07^{ns}	-13.73*	0.37^{ns}
S.E.	3.53	0.99	5.23	6.26	0.29
Female parent					
KVU 27-1	5.15^{ns}	0.27^{ns}	8.82^{ns}	-6.89^{ns}	0.50^{ns}
NE 50	11.57**	1.09^{ns}	-11.27^{ns}	11.75^{ns}	-0.34^{ns}
NE 6	14.52**	1.04^{ns}	-14.14*	13.04^{ns}	-0.62^{ns}
SECOW 2W	-12.86**	-1.06^{ns}	-0.22^{ns}	0.99^{ns}	-0.24^{ns}
SECOW 3B	-7.89^{ns}	1.31^{ns}	0.40^{ns}	-1.09^{ns}	-0.12^{ns}
WC 66	-10.48*	-2.66*	16.41*	-17.80*	0.83*
S.E.	4.32	1.21	6.40	7.67	0.36

*, **: Significance at alpha 0.05 and 0.01, respectively; ns: Not significant. S.E.: Standard error associated with GCA effects estimation

For root rot severity, ASONTEM had a negative and significant GCA effect (P<0.01), while WC 66 had a significant (P<0.05) positive GCA effect. In addition, 3 male parents (Dan 1LA, IT89KD-288 and NE 70) showed positive but non-significant GCA effects for root rot severity, while all the intermediate resistant parents (NE 50, NE 6, SECOW 2W and SECOW 3B) had negative but non-significant GCA effects.

Specific combing ability (SCA) effects of F_1 crosses for resistance to *F. redolens*

Specific combining ability effects are shown in Table 4. The results indicated non-significant SCA effects of all the crosses for percentage of dead plants and percentage of plants with lateral roots. A highly significant (P<0.001) negative SCA effect was recorded in the cross Dan 1LA × WC 66, while Dan 1LA × SECOW 2W and IT89KD-288 × WC66 had positive and significant (P<0.05) SCA effects for percentage of germination. For the amount of chlorophyll in the leaves, the cross Dan 1LA × WC 66 had a negative and significant (P<0.01) SCA effects, while the same cross had a positive and significant (P<0.05) SCA effect for root rot severity. The general observation on root rot severity of *F. redolens* showed that the crosses NE 70 × WC 66, Dan 1LA × NE 6 and Dan 1LA × SECOW 2W had the most negative but non-significant SCA effects.

Mean performance of 10 parental genotypes and 24 F1s in response to *F. redolens* infection

Genotypic mean performance (Table 5) indicated that genotype NE 70 had higher root rot severity scores and index of susceptibility (IS) mean than was expected since it was selected as a resistant parent. However, 3 resistant parents showed desirable performance with all having an IS score below 3.65. On average, none of the progeny families performed better than their resistant parents in the specific crosses, but were noticed to lean more towards the susceptible parents. In fact, some crosses like Dan 1LA × WC 66, NE 70 × KVU 27-1, NE 70 × SEC 3B and NE 70 × NE 6 had a greater value of IS than their susceptible parents.

Degree of dominance of F_1 crosses for resistance to *F. redolens*

Degree of dominance (d/a) results of the various traits considered in the study are presented in Table 6. Results from germination percentage had 7 crosses with d/a<0. The cross Dan 1LA × WC 66 had the most negative d/a (-2.76), while the cross Dan 1LA × SECOW 2W had the most positive d/a (2877.31). Considering the amount of chlorophyll in the leaves, 7 crosses had d/a<0 with the cross NE 70 × NE 50 being the most negative (d/a= -4.66), while 4 crosses had d/a>1 with the cross ASONTEM × SECOW 3B having the most positive d/a (2.81). The percentage of dead plants indicated that 19 crosses had d/a>1 with the cross NE 70 × NE 6 being the most positive d/a (5.43). In regards to percentage of plants with lateral roots, it was revealed that 16 crosses had d/a<1 with the cross NE 70 × SECOW 3B having the most negative d/a (-13.63), while the cross NE 70 × NE 50 had d/a>1. Results of root rot severity revealed that 20 F_1 crosses had d/a>0. For this parameter, it was observed that the cross NE 70 × NE 6 had the most

Table 4. Specific combing ability effects of F_1 crosses for resistance to F. redolens.

Crosses	Germination (%)	Chlorophyll amount	Dead plants (%)	Lateral roots (%)	Root rot severity
ASONTEM × KVU 27-1	-4.18^{ns}	-0.65^{ns}	-11.56^{ns}	-2.06^{ns}	-0.29^{ns}
ASONTEM × NE 50	-0.34^{ns}	-1.18^{ns}	-0.85^{ns}	-9.73^{ns}	0.18^{ns}
ASONTEM × NE 6	-3.28^{ns}	-1.96^{ns}	-2.01^{ns}	0.08^{ns}	-0.05^{ns}
ASONTEM × SECOW 2W	-16.38^{ns}	-0.38^{ns}	12.48^{ns}	10.75^{ns}	0.07^{ns}
ASONEM × SECOW 3B	14.37^{ns}	1.54^{ns}	8.92^{ns}	-5.57^{ns}	0.39^{ns}
ASONTEM × WC 66	9.81^{ns}	2.62^{ns}	-6.98^{ns}	6.54^{ns}	-0.30^{ns}
Dan 1LA × KVU 27-1	-7.57^{ns}	1.52^{ns}	2.33^{ns}	13.48^{ns}	-0.10^{ns}
Dan 1LA × NE 50	9.39^{ns}	3.63^{ns}	-1.45^{ns}	-5.13^{ns}	-0.26^{ns}
Dan 1LA × NE 6	13.59^{ns}	1.74^{ns}	-12.29^{ns}	-6.92^{ns}	-0.56^{ns}
Dan 1LA × SECOW 2W	19.54*	1.77^{ns}	-10.61^{ns}	16.64^{ns}	-0.42^{ns}
Dan 1LA × SECOW 3B	5.05^{ns}	-2.21^{ns}	-2.57^{ns}	-7.91^{ns}	-0.32^{ns}
Dan 1LA × WC 66	-39.99***	-6.45**	24.58^{ns}	-10.16^{ns}	1.67*
IT89KD-288 × KVU 27-1	6.52^{ns}	-1.11^{ns}	-6.61^{ns}	-4.45^{ns}	-0.23^{ns}
IT89KD-288 × NE 50	-9.08^{ns}	0.87^{ns}	9.46^{ns}	0.42^{ns}	0.30^{ns}
IT89KD-288 × NE 6	1.91^{ns}	-0.06^{ns}	8.38^{ns}	4.41^{ns}	-0.19^{ns}
IT89KD-288 × SECOW 2W	-6.42^{ns}	-0.23^{ns}	1.43^{ns}	-21.50^{ns}	0.46^{ns}
IT89KD-288 × SECOW 3B	-10.32^{ns}	-1.29^{ns}	-7.87^{ns}	27.59^{ns}	-0.04^{ns}
IT89KD-288 × WC 66	17.39*	1.82^{ns}	-4.79^{ns}	-6.47^{ns}	-0.30^{ns}
NE 70 × KVU 27-1	5.24^{ns}	0.24^{ns}	15.84^{ns}	-6.97^{ns}	0.61^{ns}
NE 70 × NE 50	0.03^{ns}	-3.32^{ns}	-7.17^{ns}	14.44^{ns}	-0.22^{ns}
NE 70 × NE 6	-12.22^{ns}	0.28^{ns}	5.92^{ns}	2.44^{ns}	0.80^{ns}
NE 70 × SECOW 2W	3.26^{ns}	-1.16^{ns}	-3.30^{ns}	-5.89^{ns}	-0.10^{ns}
NE 70 × SECOW 3B	-9.10^{ns}	1.95^{ns}	1.51^{ns}	-14.11^{ns}	-0.03^{ns}
NE 70 × WC 66	12.79^{ns}	2.02^{ns}	-12.81^{ns}	10.09^{ns}	-1.07^{ns}
S.E.	8.64	2.42	12.80	15.33	0.71

*, **, ***: Significance at alpha 0.05, 0.01 and 0.001, respectively; ns: Not significant. S.E.: Standard error associated with SCA effects estimation.

positive d/a (2.36). Moreover, 3 out of the 4 negative d/a for root rot severity were observed in the crosses where ASONTEM was the male parent. Averagely, the d/a for germination percentage was greater than 1, while for percentage of plants with lateral roots was less than 0, but greater than -1. The average d/a for percentage of dead plants, amount of chlorophyll in the leaves and root rot severity was greater than 0, but less than 1.

DISCUSSION

The high significant difference observed among the crosses' performance was indicative of high Genetic diversity among the parental lines and their progenies. Thus selection can be made among these genotypes for genetic improvement of the parameters studied. Besides, there was significant difference observed for GCA mean of squares of both male and female parents for all the traits suggesting that the resistance of cowpea to *F. redolens* is mainly controlled by additive

Table 5. Means of the parents and their progeny classified into resistant/susceptible classes based on IS.

Genotype	Germination (%)	Chlorophyll amount	Dead plants (%)	Lateral roots (%)	Root rot severity	IS	Reaction
IT89KD-288	26.19	36.34	0.77	100.00	3.58	3.37	R
Dan 1LA	57.14	39.48	1.49	89.06	2.88	3.40	R
ASONTEM	80.81	35.47	0.36	93.92	2.78	3.64	I
IT89KD-288 × SEC 3B	65.36	34.66	4.81	73.82	5.35	4.29	I
ASONTEM × NE 6	95.24	34.77	7.91	75.66	3.88	4.32	I
IT89KD-288 × NE 6	100.00	35.61	6.51	64.75	4.69	4.45	I
Dan 1LA × NE 6	100.00	36.97	2.55	52.82	4.64	4.50	I
IT89KD-288 × NE 50	86.07	36.59	10.48	59.49	5.46	4.58	I
ASONTEM × NE 50	95.24	35.60	11.95	64.56	4.40	4.60	I
Dan 1LA × NE 50	92.86	38.91	16.27	53.33	5.22	4.65	I
NE 70	61.90	35.25	0.54	45.17	4.04	4.79	I
NE 6	99.37	32.37	4.15	59.44	5.19	4.83	I
Dan 1LA × SEC 2W	78.57	34.90	18.15	64.35	5.16	4.83	I
NE 70 × NE 50	97.39	30.16	1.91	60.08	5.23	4.97	I
ASONTEM × SEC 3B	90.48	38.54	33.38	55.88	4.82	5.06	I
ASONTEM × KVU 27-1	84.97	35.31	21.32	53.59	4.78	5.12	I
ASONTEM × SEC 2W	54.76	34.25	36.32	74.29	4.38	5.13	I
NE 70 × NE 6	88.08	33.70	12.13	49.36	5.97	5.13	I
ASONTEM × WC 66	83.33	35.64	33.50	51.28	5.08	5.45	I
IT89KD-288 × KVU 27-1	95.24	33.80	14.48	35.97	5.78	5.49	I
Dan 1LA × KVU 27-1	69.47	35.98	40.13	53.31	6.23	5.54	I
IT89KD-288 × SEC 2W	64.29	33.34	13.49	26.81	5.72	5.72	I
Dan 1LA × SEC 3B	69.05	33.29	26.81	37.71	5.38	5.81	I
NE 50	80.74	33.45	17.97	26.26	5.59	5.84	I
SECOW 3B	96.41	32.08	35.83	49.36	6.06	5.89	I
NE 70 × SEC 3B	68.80	35.65	22.26	18.69	5.64	5.91	I
IT89KD-288 × WC 66	90.48	33.79	23.90	23.04	6.04	6.03	I
NE 70 × SEC 2W	76.19	30.16	16.83	28.98	5.44	6.06	I
NE 70 × WC66	88.10	31.74	23.95	26.17	5.55	6.15	I
SECOW 2W	57.13	29.06	29.82	36.17	6.46	6.33	I
KVU 27-1	92.86	31.40	29.71	10.24	6.89	6.70	S
NE 70 × KVU 27-1	96.18	32.90	45.01	20.03	6.90	6.72	S
WC 66	97.62	27.22	30.04	6.87	7.08	7.19	S
Dan 1LA × WC 66	21.43	25.08	69.97	18.75	8.32	8.14	S
CV (%)	24.91	9.14	79.72	48.68	21.66	19.63	-
LSD (P=0.05)	18.78	4.80	25.32	30.33	1.41	0.60	-

R: Resistant, I: Intermediate; S: Susceptible; n= 34, GM: Grand mean, CV: Coefficient of variation, LSD: Least significant difference.

Table 6. Degree of dominance for resistance of F_1 crosses *to F. redolens*.

Genotype	Germination (%)	Chlorophyll amount	Dead plants (%)	Lateral roots (%)	Root rot severity
ASONTEM × KVU 27-1	-0.31	0.92	0.43	0.04	-0.03
ASONTEM × NE 50	431.75	1.12	0.32	0.13	0.15
ASONTEM × NE 6	0.55	0.55	2.99	-0.06	-0.08
ASONTEM × SECOW 2W	-1.2	0.62	1.44	0.32	-0.13
ASONTEM × SECOW 3B	0.24	2.81	0.86	-0.71	0.24
ASONTEM × WC 66	-0.7	1.04	1.23	0.02	0.07
Dan ILA × KVU 27-1	-0.31	0.13	1.74	0.36	0.67
Dan ILA × NE 50	2.03	0.81	0.79	-0.24	0.73
Dan ILA × NE 6	1.03	0.29	-0.2	-0.62	0.53
Dan ILA × SECOW 2W	2877.31	0.12	0.18	0.07	0.27
Dan ILA × SECOW 3B	-0.39	-0.67	0.47	-1.06	0.57
Dan ILA × WC 66	-2.76	-1.35	3.8	-3.44	1.59
IT89KD-288 × KVU 27-1	1.07	-0.03	-0.05	-0.44	0.33
IT89KD-288 × NE 50	1.2	1.18	0.13	-0.13	0.87
IT89KD-288 × NE 6	1.02	0.63	2.4	-0.75	0.38
IT89KD-288 × SECOW 2W	1.46	0.18	-0.12	-1.28	0.49
IT89KD-288 × SECOW 3B	0.12	0.21	-0.77	-0.08	0.42
IT89KD-288 × WC 66	0.8	0.44	0.58	-0.66	0.40
NE 70 × KVU 27-1	1.21	-0.22	2.05	-0.44	1.01
NE 70 × NE 50	2.77	-4.66	-0.84	2.58	0.53
NE 70 × NE 6	0.4	-0.07	5.43	-0.41	2.36
NE 70 × SECOW 2W	6.98	-0.64	0.11	-2.6	0.16
NE 70 × SECOW 3B	-0.6	1.25	0.23	-13.63	0.58
NE 70 × WC66	0.47	0.13	0.59	0.01	-0.01
Average d/a	138.50	0.20	0.99	-0.96	0.50

genetic effects. Since the male parent was expected to pass resistance and female parent to pass susceptibility, this would mean that both resistance and susceptibility genes were passed on to the progeny. In addition to the GCA effects, SCA mean of squares were also significant for percentage of germination and amount of chlorophyll in the leaves implying that these two traits were controlled by both additive and non-additive genetic effects. In contrast, SCA mean of squares were not significant for percentage of dead plants, percentage of plants with lateral roots and root rot severity. These implied that the non-additive genetic effects had minor influence on these traits and additive gene action provided a larger contribution in the crosses than the non-additive gene action. This was further confirmed by the relatively high values of Baker's ratio (BR >0.71) that were observed for these traits, suggesting that the performance of the progeny could be accurately predicted based on the parental GCA effects as reported by Baker (1978) and Bernardo (2002). As far as percentage of germination and chlorophyll amount are concerned, the non-additive genetic effects were predominant over the additive, hence poor predictability of the progeny's performance.

The estimated moderate h^2 indicated that about 50% of the total phenotypic variation observed for percentage of dead plants, % of plants with lateral roots and root rot severity, was due to additive genes effects. These results suggested that selection at early generation would be fairly effective for improving *F. redolens* resistance in cowpea as outlined by Baker (1978) and Piepho and Möhring (2007).

Earlier studies have proven that lateral roots are very essential to the complexity of resistance to root rots (Snapp et al., 2003). However, in order to target this trait for improvement of resistance to *F. redolens* through breeding, it is essential to consider parents that exhibit high frequency of lateral roots. For percentage of germination and amount of chlorophyll, h^2 was low, suggesting that additive genes had a small contribution to the overall phenotypic variation; hence, selection would be more appropriate at advanced generation. Further observations revealed that genotypes which developed cracks on the testa were highly vulnerable to seed rot. Accordingly, Souza and Marcos-Filho (2001), seed coat traits (e.g. permeability) which determines the ability of the seed to resist fungal rots are influenced by both genetic and environmental effects. Earlier study by Ismail et al. (2000) into stay green traits led to the conclusion that the ability of cowpea to retain chlorophyll (delayed leaf senescence) in stressed condition is highly correlated to its resistance to pathogenic *Fusarium* spp. These results are consistent with their findings where the materials (parents/crosses) that showed moderate to high resistance retained high chlorophyll amount throughout the test period.

The parents NE 50 and NE 6 showed positive and desirable significant GCA effects for high germination and therefore were associated with resistance to seed rot caused by *F. redolens* showing that they are good combiners for improvement of this trait. On the contrary, Dan 1LA, SECOW 2W, SECOW 3B and WC 66 had negative GCA effects for low germination and therefore were not associated with resistance to seed rot caused by *F. redolens* implying that they are poor combiners for improvement of this trait. Likewise, WC 66 significantly contributed to reduced leaf chlorophyll level, reduced lateral roots but increased mortality of plants and increased root rot severity in its progenies due to *F. redolens* infection. The genotype NE 70 with a negative and significant GCA effect contributed to the reduction of susceptibility of cowpea plant mortality in its progenies thus making it a good combiner for this trait. However, NE 70 had a negative and significant GCA effect for percentage of plants with lateral roots implying that its crosses would have reduced lateral roots thus become vulnerable to *F. redolens* infection. On the other hand, ASONTEM had significant positive GCA for lateral roots and negative for root rot severity making it a good combiner for improving these two traits. The other male parents had positive but non-significant GCA effects for root rot severity. This indicated that there is a possibility of these parents passing susceptibility to root rot to their progenies. Contrastingly, all the intermediate resistant parents had negative GCA effects for root rot severity which implied they were good combiners and would pass resistance to root rots to their progenies.

The cross Dan 1LA × WC 66 with undesirable SCA effects for all the traits was a poor combination in all the traits. These undesirable observed SCA effects observed indicated that the cross's performance was below what could be predicted from the GCA effects of the parents (Bernardo, 2002; Falconer and Mackay, 1996). Contrary to this, IT89KD-2288 × WC 66 showed a positively significant SCA effect for percentage of germination making it a good combination as the progeny had 17.39% better germination than the expected germination. Moreover, several crosses showed negative but non-significant SCA effects for root rot severity which indicated they could be good combiners.

The results of parental means saw 2 of the parents (ASONTEM and NE 70) performing lower than had been recorded in previous study. This could be attributed to higher levels of inoculum in the soil that might have affected their response to the pathogen especially in relation to lateral roots production. Moreover, the progenies were observed to perform poorer than the resistant parents. The results from the d/a indicated an average over dominance for high germination percentage ($d/a>1$) and an average partial dominance for high amount of chlorophyll in the leaves ($0<d/a<1$), high percentage of dead plants ($0<d/a<1$), low percentage of plants with lateral roots ($-1<d/a<0$) and high root rot severity (susceptibility) ($0<d/a<1$) in accordance with the description provided by Kearsey and Pooni (1996) and Falconer and Mackay (1996). This implies that for the parameters considered in this study, the favourable alleles contributing to high germination percentage and high amount of chlorophyll in the leaves were dominantly inherited while the alleles of low percentage of dead plants, high percentage of plants with lateral roots and low root rot severity (resistance) were recessively inherited as observed by the values of average d/a. The high frequency of crosses showing desirable over dominance for germination percentage, suggests that there was great possibility for improvement through selection methods by targeting those crosses that showed better performance than the better parent (Rieseberg et al., 1999). In contrast, the traits with recessive favourable alleles require extensive testing at a segregating generation to select progenies with desirable phenotypes. The cross Dan 1LA × WC66 showed over dominance towards susceptibility to *F. redolens*, thus provided poor combination when all the traits are considered. Furthermore, the combination of Dan 1LA and WC 66 led to poor seed development that was coupled with cracks on the testa and these paved ways to early infection leading to low germination and high

mortality of plants at early stages of growth. Souza and Marcos-Filho (2001) emphasized on the importance of seed coat in protecting the seed from infection, a factor that was confirmed in this study.

Conclusion

Dead plants percentage, lateral roots percentage, and root rot severity were found to be majorly conditioned by additive genetic effects, while both additive and non-additive gene effects were involved in the inheritance of genes leading to increased germination and amount of leaf chlorophyll. Early-generation selection could be effective for percentage of dead plants, percentage lateral roots and root rot severity, while selection at advanced would be preferable for percentage germination and amount of leaf chlorophyll. Genotypes, NE 50 and NE 6 were the best combiners for percentage germination, while ASONTEM was the best combiner for percentage lateral roots and root rot severity as observed from GCA effects. These parents with desirable GCA effects for particular traits should be incorporated into breeding programmes and used for improving the other genotypes so as to achieve better resistance to *F. redolens.*

Response to plant mortality, lateral roots production and resistance root rot were found to be recessively inherited, while percentage germination and level of chlorophyll in the leaves were dominantly inherited. Moreover, the cross Dan 1LA × WC 66 had the worst performance across all the traits with net over-dominance towards susceptible parent being recorded and significantly undesirable SCA effects for percentage germination, amount of leaf chlorophyll and root rot severity. Contrary to this, the cross Dan 1LA × SECOW 2W and IT89KD-288 × WC 66 had significant positive SCA effects in percentage of germination showing that they are good combination for this trait.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Genetic variability, correlation and path analysis of yield and grain quality traits in bread wheat (*Tritium aestivum* L.) genotypes at Axum, Northern Ethiopia

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Forty-nine bread wheat genotypes were tested at Axum, Northern Ethiopia in 2016/17, with the objective of assessing the extent of genetic variation, correlation and path analysis of wheat genotypes in yield and grain quality traits using 7 x 7 triple lattice design. Data were collected for 17 agronomic and grain quality characters. For each of the test entries, samples of 500 g grains were taken from each plot for quality analysis. The NIR spectrophotometer (NIR Infratec 1241 Grain analyzer, Sweden) was used to analyze wheat samples for their protein, wet gluten, zeleny sedimentation volume and starch content based on dry weight basis. Data were subjected to analysis of variance which revealed significant differences among the genotypes for all the characters. The genotypic coefficient of variation (GCV) ranged from 1.63 (for starch content) to13.30% (for grain yield). The broad sense heritability (H^2) ranged from 15.89 (for number of tillers) to 97.16% (for days to heading), while genetic advance as percent of mean (GAM) from 2.01 (for starch content) to 19.63% (for days to heading). The GCV and phenotypic coefficient of variation (PCV) differences were low in magnitude for days to heading and days to maturity, and H^2 values were coupled with moderate to high GAM. This suggests selection based on phenotype of genotypes could be effective to improve these characters. Grain yield was positively and significantly correlated with biological yield (0.72), harvest index (0.65), plant height (0.51), thousand kernel weight (0.31), hectoliter weight (0.37) and starch content (0.32), of which biomass yield (0.85) and harvest index (0.70) had the highest positive direct effect on grain yield. Thus, selection for higher mean values of biomass yield and harvest index could be considered simultaneously for selection of higher grain yield.

Key words: Bread wheat, correlation, genetic coefficient of variation, genetic advance, grain quality, heritability.

INTRODUCTION

Wheat is one of the most important export and strategic cereal crops in the world and in Ethiopia in terms of production and utilization (Suresh, 2013). It is the second most important staple food crop of the world; it provides more calories in human diet than any other crop worldwide. It accounts for nearly 30% of global cereal

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production, covering an area of 222.42 million hectares with total production of 725.12 million tons (FAO, 2015). Given its predominance in human diets, cultivated wheat has to meet the specific quality criteria for the manufacture of a wide range of food products derived from it.

Wheat is one of the most important small cereal crops in Ethiopia, which ranks fourth both in area coverage (1,663,845.63 hectares) and in total annual production (4,231,588.716 tons). The productivity of the crop remains low (2.54 t ha^{-1}) (CSA, 2015) in the country as compared to the world average yield (3.19 t ha^{-1}) (FAO, 2013). The low yield per hectare is attributed to many factors, such as unavailability of quality seed for varieties that are high yielding as well as adapted to wide range of agro-ecologies of the country. Hence, the first step in the development of varieties is assessing the genetic variability of available genotypes for the characters of interest (Rahman et al., 2016). High genetic advancement coupled with high heritability estimates offers the most suitable condition for selection (Johnson et al., 1955). The presence of variability, heritability and genetic advance in different yield related characters of bread wheat has been reported by Desalegn and Chauhan (2016), Kifle et al. (2016) and Rahman et al. (2016). However, no variability studies have been conducted in the study area. Moreover, the variability studies in the region were not on moisture stress tolerant bread wheat genotypes. In addition, genetic information is limited to grain quality traits in bread wheat genotypes evaluated in the country. Considering the importance of such information, this research was initiated with the objective of assessing genetic variability for yield and grain quality traits, and determining the association among the yield components of bread wheat genotypes.

MATERIALS AND METHODS

Field experiment was conducted at Axum Agricultural Research Center (AxARC), Northern Ethiopia during 2016-2017. The experimental site is located at latitude 13°15'40.2" N, and 38°34'45.8'' E longitudes with an altitude of 2148 m above sea level. It is characterized by uni-modal rainfall pattern concentrated in one season from July to August with total annual rain fall of 500 to 782.8 mm per annum. The mean minimum and maximum temperatures ranged from 12.6 to 25.51°C, respectively. The soil type of the site is clay type with pH ranging from7.5 to 8.3. A total of 49 bread wheat genotypes introduced from ICARDA-CIMMYT (Table 1) were included in the study. The experiment was laid down in 7x7 triple lattice design. Each genotype was planted in a plot consisting of six rows of 2.5 m long and 1.2 m width; a total of 3 m^2 with spacing of 20 cm between rows. The distances between plots, blocks and replications were 0.5, 0.5 and 1.5 m, respectively. A seed rate of 150 kg ha^{-1} and fertilizer rate of 100-100 kg ha^{-1} N-P_2O_5 in the forms of Urea and DAP (di -ammonium phosphate) were used.

For each of the test entries, samples of 500 g grains were taken from each plot for quality analysis. The NIR spectrophotometer (NIR Infratec 1241 Grain analyzer, Sweden) was used to analyze wheat samples for their protein, wet gluten, zeleny sedimentation, starch content and moisture content based on dry weight basis. While, hectoliter weight was estimated using grain analyzer computer 2100.

Data collected

Data were collected both from plot and plant basis. The four central rows were used for data collection based on plots, such as days to 50% heading, days to physiological maturity, grain yield, biomass yield and harvest index. Ten randomly selected plants from the four central rows of each plot were used for data collection on plant basis and the averages of the ten plants in each experimental plot were used for statistical analysis for traits such as plant height, productive tillers per plant, number of kernels per spike, number of spike lets per spike and spike length.

Data for grain quality traits

For each of the test entries, samples of 500 g were taken from each plot for quality analysis and the NIR spectrophotometer (NIR Infratec 1241 Grain analyzer, Sweden) was used to analyze wheat samples.

Statistical analysis

The mean values of the genotypes were subjected to analysis of variance based on triple lattice design. Analysis of variance was done using Proc lattice and Proc GLM procedures of SAS version 9.1.3 (SAS Institute Inc, 2004) after testing the ANOVA assumptions. Mean separations were estimated using Duncan's multiple range (DMRT) test at 5% probability levels.

Estimation of variance components and association among characters

The phenotypic and genotypic coefficients of variation were estimated according to the methods suggested by Burton and De Vane (1953).

$$PCV = \frac{\sqrt{\sigma 2\,p}}{\bar{X}} * 100$$

Where, σ^2 p = phenotypic variance and $\bar{X}$ = mean of the characters evaluated.

$$GCV = \frac{\sqrt{\sigma 2\,g}}{\bar{X}} \times 100$$

Where, σ^2g = genotypic variance, $\bar{x}$ = mean of the characters evaluated. Broad sense heritability was computed for each character based on the formula developed by Allard (1960) as: $H^{2=} \frac{\sigma 2g}{\sigma 2p} \times 100$

The genetic advance (GA) for selection intensity (K) at 5% was calculated by the formula suggested by Allard (1960) as:

$$GA = K * \sigma_p * H^2$$

Where, GA = Expected genetic advance, σ_p = the phenotypic standard deviation, H^2 = broad sense heritability, K= selection differential (K=2.06 at 5% selection intensity).

$$GA \text{ (as \% of the mean) (GAM)} = \frac{GA}{\bar{X}} \times 100$$

Where $\bar{x}$= population mean.

Table 1. Genotypes used in the study.

Name	Pedigree
ETBW8484	MUTUS//WBLL1*2/BRAMBLING/3/WBLL1*2/BRAMBLING
ETBW8486	SNLG/3/EMB16/CBRD//CBRD/4/KA/NAC//TRCH
ETBW9019	MUTUS//KIRITATI/2*TRCH/3/WHEAR/KRONSTAD F2004
ETBW9026	AGUILAL/FLAG-3
ETBW9027	REYNA-29
ETBW9028	MUTUS//ND643/2*WBLL1
ETBW9029	ND643/2*WBLL1/4/CHIBIA//PRLII/CM65531/3/SKAUZ/BAV92/5/BECARD
ETBW9033	DANPHE #1*2/CHYAK
ETBW9034	MUTUS*2/HARIL #1
ETBW9040	T.DICOCCON CI9309/AE.SQUARROSA (409)// MUTUS/3/2*MUTUS
ETBW9042	HUW234+LR34/PRINIA//PFAU/WEAVER/3/CMH83.30
ETBW8489	VORB/6/CPI8/GEDIZ/3/GOO//ALB/CRA/4/AE.SQUARROSA (208)/5/2*WESTONIA/7/ CPI8/ GEDIZ/3/GOO//ALB/CRA/4/AE.SQUARROSA (208)/5/2*WESTONIA
ETBW8492	KRICHAUFF/2*PASTOR//CHONTE
ETBW9015	SUP152//ND643/2*WBLL1/3/ND643/2*WBLL1
ETBW9016	SWSR22T.B./2*BLOUK #1//WBLL1*2/KURUKU
ETBW9017	SWSR22T.B./2*BLOUK #1//WBLL1*2/KURUKU
ETBW9018	SWSR22T.B.//TACUPETO F2001*2/ BRAMBLING/3/2*TACUPETO F2001*2/ BRAMBLING
ETBW9041	T.DICOCCON CI9309/AE.SQUARROSA (409)//MUTUS/3/2*MUTUS
ETBW9051	CROC-1/AE.SQUARROSA (224) //OPATA/3/QAFZAH-21/4/SOMAMA-3
ETBW 8471	WEEBILL-1/BOCRO-3
ETBW 8472	SANOBAR-4
ETBW 8473	SUNCO.6/FRAME//PASTOR/3/PAURAQ
ETBW 8474	1447/PASTOR//KRICHAUFF/3/PAURAQ
ETBW 8475	WORRAKATTA/2*PASTOR//DANPHE #1
ETBW 8476	1447/PASTOR//KRICHAUFF/5/2*SERI*3//RL6010/4*YR/3/PASTOR/4/BAV92
ETBW 8477	C80.1/3*BATAVIA//2*WBLL1/3/EMB16/CBRD//CBRD/4/CHEWINK #1
ETBW 8478	SLVS/3/CROC_1/AE.SQUARROSA(224)// OPATA/5/VEE/LIRA//BOW/3/BCN/4/KAUZ/6/2*KA/NAC//TRCH
ETBW 8479	METSO/ER2000//MUU
ETBW 8480	KA/NAC//TRCH/3/DANPHE #1
ETBW 8481	EMB16/CBRD//CBRD/4/BETTY/3/CHEN/AE.SQ//2*OPATA
ETBW 6861	WAXWING*2/HEILO
ETBW 8506	AGUILAL/FLAG-3
ETBW 8507	DURRA-4
ETBW 7120	QAFZAH-23/SOMAMA-3
ETBW 8508	REYNA-8
ETBW 7213	CHAM-4/SHUHA'S'/6/2*SAKER/5/RBS/ANZA/3/KVZ/HYS//YMH/TOB
ETBW 8509	REYNA-29
ETBW 7038	ATTILA/3*BCN//BAV92/3/TILHI/5/BAV92/3/PRL/SARA// TSI/VEE#5/4/CROC_1/AE.SQUARROSA (224)//2*OPATA
ETBW 8510	HIJLEEJ-1
ETBW 8511	BOW #1/FENGKANG 15/3/HYS//DRC*2/7C
ETBW 7147	CROC-1/AE.SQUARROSA(224)// OPATA/3/QAFZAH-21/4/SOMAMA-3
ETBW 8512	BABAX/LR42//BABAX*2/3/KURUKU/4/KINGBIRD #1
ETBW 7871	PAURAQ/4/PFAU/SERI.1B//AMAD/3/WAXWING
ETBW 8513	MUTUS//WBLL1*2/BRAMBLING/3/WBLL1*2/BRAMBLING
ETBW 6940	UTIQUE 96/FLAG-1
Kakaba (PICAFLOR#1)	Kititati//Seri/Rayon
Shorima (ETBW5483)	UTQE96/3/PYN/BAU//Milan
Ogolcho(ETBW5520)	WORRAKATTA/2*PASTOR
King bird	THELIN # 2/TUKURU

Table 2. Mean squares from analysis of variance for the 17 characters of 49 bread wheat genotypes.

Characters	Mean square						RE to RCBD(%)	CV (%)
	Replication (2)	Treatments (48)		Blocks with in rep(Adj) (18)	Error			
		Un-adj	Adj		Intra(78)	RCBD(96)		
DH	51.76	98.19	83.48**	1.39	0.98	1.06	102.12	1.71
DM	40.62	187.40	169.58**	6.48	8.34	7.99	95.82	2.83
GFP	56.63	43.01	43.42**	7.99	5.28	5.79	103.08	5.22
PH(cm)	60.41	97.33	86.58**	14.92	15.66	15.52	99.11	4.92
NT	0.07	0.23	0.21*	0.23	0.13	0.14	105.98	18.75
KPS	9.69	89.63	82.98**	14.95	22.44	21.03	93.74	10.13
SKPS	0.17	4.49	3.80**	1.12	0.83	0.88	101.69	5.63
SL(cm)	0.26	0.91	0.76**	0.19	0.25	0.23	95.55	5.98
BY(t ha^{-1})	20.89	4.39	3.71**	1.02	1.26	1.22	96.40	12.00
GY(t ha^{-1})	5.28	1.14	0.97**	0.21	0.25	0.24	97.20	12.53
HI(%)	33.55	71.25	62.61*	32.78	35.45	34.95	98.59	13.91
TKW(g)	58.07	32.80	30.59**	8.68	5.67	6.24	103.24	7.00
HLW	4.85	10.72	10.34**	3.09	2.27	2..42	101.70	1.92
GPC(%)	5.12	1.89	1.70**	0.61	0.47	0.49	101.23	4.95
WG(%)	23.78	14.99	14.13**	3.55	3.41	3.44	100.03	5.85
ZSV(%)	78.77	54.40	46.49**	8.33	11.91	11.24	94.37	7.15
SC(%)	1.89	2.39	2.20**	0.38	0.42	0.41	98.50	1.02

ns= Non-significant,* and ** = significant at 5 and 1% probability level, respectively. Number in parenthesis represented degree of freedom. DH= days to heading, DM = days to maturity, GFP = grain filling period, PH = plant height, NT = number of productive tillers per plant, KPS = number of kernels per spike, SPKS = number of spike lets per spike, SL= spike length, BY= biomass yield, GY= grain yield, HI = harvest index, TKW = thousand kernel weight, HLW = hectoliter weight, GPC = grain protein content, WG = wet gluten, ZSV = zeleney sedimentation value and SC = starch content, ETBW= Ethiopian bread wheat, adj= adjusted, SE= standard error.

Correlation coefficient

Estimation of genotypic and phenotypic correlation coefficients was done based on the procedure of Dabholkar (1992).

Path coefficient analysis

Path coefficient analysis which refers to the estimation of direct and indirect effects of the yield attributing characters on grain yield was calculated based on the method used by Dewey and Lu (1959) as follows:

$rij = Pij + \Sigma rik\ pkj$

The residual effect, which determines how best the causal factors account for the variability of the dependent factor yield, was computed using the formula:

$1=p^2R + \Sigma\ p\ ij\ rij$

Where, p^2R is the residual effect; p ij rij = the product of direct effect of any variable and its correlation coefficient with yield.

RESULTS AND DISCUSSION

The mean values for 17 characters of 49 bread wheat genotypes are presented in Appendix Table 1.

Genotypes had in between 49 to 73.33 days to heading and 87 to 118 days to maturity with a mean of 57.99 and 101.83 days, respectively. The result showed a wide range of variations for days to heading and maturity. Grain yield ranged from 2.37 to 5.44 t ha^{-1} with a mean of 3.95 t ha^{-1}. Maximum grain yield was obtained from the genotypes ETBW9016 (5.44 t ha^{-1}), ETBW8480 (5.37 t ha^{-1}), ETBW8475 (4.64 t ha^{-1}) and ETBW8486 (4.56 t ha^{-1}). Grain protein content ranged from 11.93% for the check variety King bird to 15.43% for ETBW8489 with a mean value of 13.79%.

Mean squares of 17 characters from analysis of variance (ANOVA) are presented in Table 2. The analysis of variance showed highly significant (P<0.01) differences among genotypes for all the characters except number of effective tillers per plant and harvest index in which genotypes had significant differences (P<0.05). Significant genetic variation among genotypes for various characters suggested that the genotypes were genetically diverse and could be a good opportunity for breeders to select genotypes for trait of interest. Several researchers reported significant differences among bread wheat genotypes studied (Kifle et al., 2016; Kumar et al., 2016; Tesfaye et al., 2016; Birhanu et al., 2016).

Table 3. Phenotypic and genotypic variances and coefficients of variations, heritability in broad sense and genetic advance for 17 characters of 49 bread wheat genotypes

Characters	Ranges	Mean ± SE	σ^2g	PCV	GCV	H^2	GA	GAM
DH	47-74	58.17±0.47	31.52	9.79	9.65	97.16	11.42	19.63
DM	86-120	102.14±0.65	58.42	7.99	7.48	87.81	14.78	14.47
GFP	36-60	43.97±0.31	11.88	9.56	7.84	67.18	5.83	13.25
PH	64.4-98.8	80.40±0.47	26.85	8.08	6.45	63.99	8.55	10.64
NT	1.0-3.60	1.93±0.02	0.03	21.88	8.72	15.89	0.14	7.17
KPS	31.0-67.1	46.77±0.45	20.99	14.08	9.79	48.56	6.59	14.08
SKPS	11.8-20.5	16.15±0.10	1.09	8.68	6.48	55.76	1.61	9.99
SL	6.40-9.90	8.29±0.05	0.21	8.03	5.49	46.73	0.64	7.74
BY	5.50-13.0	9.29±0.10	0.99	15.81	10.64	45.29	1.38	14.77
GY	2.37-5.44	3.95±0.05	0.28	18.21	13.30	52.83	0.79	19.94
HI	26.4-51.5	42.49±0.40	11.70	16.03	7.99	24.83	3.52	8.21
TSW	26.3-43.6	34.01±0.27	8.09	11.04	8.45	57.41	4.45	13.08
HLW	73.0-82.7	78.67±0.16	2.49	2.84	2.00	49.77	2.29	2.92
GPC	11.9-15.4	13.79±0.07	0.42	6.88	4.71	46.86	0.92	6.65
WG	27.2-36.5	31.49±0.18	3.74	8.50	6.13	51.97	2.88	9.11
ZSV	34.4-53.1	47.9±0.35	13.02	10.19	7.48	53.83	5.46	11.32
SC	61.1-65	62.9±0.07	0.63	1.63	1.26	60	1.27	2.01

DH= Days to heading, DM = days to maturity, GFP = grain filling period, PH = plant height, NT = number of productive tillers per plant, KPS = number of kernels per spike, SPKS = number of spike lets per spike, SL= spike length, BY= biomass yield, GY= grain yield, HI = harvest index, TKW = thousand kernel weight, HLW = hectoliter weight, GPC = grain protein content, WG = wet gluten, ZSV = zeleney sedimentation value and SC = starch content, σ^2g= genetic variance, PCV= phenotypic variance, GCV= genotypic variance, GA= genetic advance, GAM= genetic advance as percent of mean.

Estimation of variability components

The estimated phenotypic coefficient of variation (PCV) and genotypic (GCV) coefficients of variations are presented in Table 3. The GCV ranged from 1.26% for starch content to 13.30% for grain yield and PCV from 1.63% for starch content to 21.88% for number of productive tillers per plant. The GCV and PCV values were categorized as low (<10%), moderate (10 to 20%) and high (>20%) as indicated by Deshmukh et al. (1986). Accordingly, moderate GCV and PCV was observed for grain yield (13.30 and 18.21%) and biomass yield (10.64 and 15.81%), respectively. This indicated that the genotype could be reflected by the phenotype and the effectiveness of selection based on the phenotypic performance for these characters. Report of Birhanu et al. (2016) is in line with the occurrence of GCV and PCV media in this study.

The PCV value was high for number of productive tillers, while medium PCV values were observed for harvest index, kernels per spike, thousand seed weight and Zeleny sedimentation value. The lowest GCV and PCV were recorded for days to heading, days to maturity, grain filling period, plant height, number of spikelets per spike, hectoliter weight, grain protein content, wet gluten content and starch content. The result indicates the environmental factors had more influence on the expression of these characters than the genetic factors, suggesting the limited scope for improvement of these characters by direct selection of high performing genotypes. This is in agreement with reports of Naik et al. (2015) and Rahman et al. (2016).

Estimation of heritability and expected genetic advance

The heritability estimates ranged from 15.89% for number of productive tillers per plant to 97.16% for days to heading. According to Singh (1990), for a character with high heritability (≥80%), selection is fairly easy, because there would be a close correspondence between genotype and phenotype due to a relatively smaller contribution of environment to phenotype. High heritability was estimated for days to heading (97.16%) and days to maturity (87.81%). This implies the variation observed was mainly under genetic control and was less influenced by the environment and the possibility of progress from selection. The obtained results are in agreement with results reported by Tesfaye et al. (2016). Moderate heritability values (40-80%) were computed for grain filling period, plant height, kernels per spike, spike lets per spike, spike length, biomass yield, grain yield, thousand kernel weight, hectoliter weight, grain protein content, wet gluten content and Zeleny sedimentation value. Low heritability (<40) estimated for number of effective tillers per plant and harvest index indicated that

Table 4. Estimation of genotypic (above diagonal) and phenotypic (below diagonal) correlation coefficient for 17 morphological and quality traits in 49 bread wheat advanced lines.

Traits	DH	DM	GFP	PH	NT	KPS	SKPS	SL	BY	GY	HI	TSW	HLW	GPC	WGC	ZSV	SC
DH	1	0.90**	0.38*	0.26	-0.5*	0.14	0.39*	0.37*	0.14	-0.19	-0.44*	-0.44*	-0.6**	-0.20	0.03	-0.17	0.19
DM	0.87**	1	0.74**	0.36*	-0.4*	0.19	0.46*	0.43*	0.22	-0.05	-0.34*	-0.35*	-0.49*	-0.30*	0.02	-0.25	0.32*
GFP	0.31*	0.74**	1	0.35*	-0.19	0.19	0.37	0.35*	0.24	0.19	-0.04	-0.08	-0.09	-0.31*	-0.01	-0.25	0.38*
PH	0.19*	0.32*	0.34**	1	-0.21	0.29*	0.20	0.12	0.58**	0.51*	0.00	0.08	-0.11	-0.48*	-0.32*	-0.31*	0.31*
NT	-0.27*	-017*	0.02	-0.12	1	-0.20	-0.36*	-0.24	-0.04	0.22	0.38*	0.40*	0.38*	0.07	0.05	0.08	-0.06
KPS	0.12	0.16	0.15	0.30*	-0.02	1	0.72**	0.33*	0.21	0.19	0.01	-0.16	-0.11	-0.30*	-0.32*	-0.17	0.04
SKPS	0.33**	0.39**	0.31*	0.25*	-0.15	0.65**	1	0.63**	0.08	0.02	-0.09	-0.33*	-0.27	-0.09	-0.07	-0.07	0.01
SL	0.28*	0.36**	0.30*	0.23*	-0.05	0.42**	0.61**	1	0.06	-0.09	-0.21	-0.03	-0.22	0.03	0.19	0.14	0.09
BY	0.05	0.15	0.22*	0.51**	-0.0	0.15	0.09	0.06	1	0.72**	-0.20	0.06	0.16	-0.43*-	-0.24	-0.27	0.34*
GY	-0.18*	-0.01	0.22*	0.47**	0.15	0.13	0.06	-0.03	0.65**	1	0.53**	0.31*	0.37*	-0.38*	-0.27	-0.23	0.32*
HI	-0.28*	-0.19*	0.04	0.02	0.30*	-0.01	-0.02	-0.11	-0.28*	0.53**	1	0.39*	0.35*	-0.01	-0.09	0.00	0.05
TSW	-0.5**	-0.23*	0.02	0.04	0.21*	-0.13	-0.25*	-0.05	0.10	0.26*	0.23*	1	0.71**	-0.04	0.05	0.11	0.34*
HLW	-0.4**	-0.27*	-0.01	-0.07	0.25*	-0.01	-0.19*	-0.11	0.15	0.29*	0.23*	0.65**	1	-0.15	-0.14	-0.06	0.31*
GPC	-0.21*	-0.27*	-0.23*	-0.25*	-0.07	-0.20*	-0.01	0.03	-0.14	-0.14	0.00	-0.14	-0.21*	1	0.81**	0.80**	-0.7**
WG	0.00	0.00	0.01	-0.14	-0.04	-0.21*	0.02	0.14	-0.05	-0.08	-0.03	-0.02	-0.13	0.81**	1	0.71**	-0.22
ZSV	-0.18*	-0.22*	-0.18*	-0.17*	0.01	-0.16*	-0.05	0.08	-0.06	-0.06	-0.00	-0.01	-0.13	0.77**	0.67**	1	-0.43*
SC	0.19*	0.32**	0.34**	0.20*	0.03	0.03	-0.00	0.07	0.19*	0.19*	0.02	0.41**	0.39**	-0.7**	-0.3**	-0.5**	1

*And **=significant at 5% and 1% probability levels, respectively. DH=days to heading, DM = days to maturity, GFP = grain filling period, NT = number of productive tillers per plant, PH = plant height, SL= spike length, SKPS = number of spike lets per spike, KPS = number of kernels per spike, BY = biomass yield, GY = grain yield, HI = harvest index, TKW = thousand kernel weight, HLW = hectoliter weight, GPC = grain protein content, WG = wet gluten content, ZSV = Zeleny sedimentation value and SC = starch content.

selection for these characters would not be effective due to the predominant effects of non-additive genes. In consonance with the current result, Desalegn and Chauhan (2016) reported low heritability for tillers per plant (26.3%) and harvest index (11.1%). It has been suggested that heritability estimates together with genetic advance are more helpful in predicting the gain under selection than heritability estimates alone in selecting best individuals because heritability does not provide indication of amount of genetic progress that would result from selecting the best individuals (Johnson et al., 1955). High heritability is coupled with moderate genetic advance as percent of mean observed for days to heading and days to maturity. This indicates that most likely the heritability of these characters is due to additive gene effects, and selection might be effective for these characters (Salman et al., 2014; Rahman et al., 2016).

Correlation of grain yield with other characters

Grain yield had positive and highly significant (P<0.01) genotypic correlation with biomass yield (0.65) and harvest index (0.53) (Table 4). Grain yield also exhibited positive and significant (P<0.05) genotypic correlation with plant height (0.51), thousand kernel weight (0.31), hectoliter weight (0.37) and starch content (0.32). The positive association of these characters with grain yield might be due to the higher assimilation of photosynthesis as biomass because of the increased plant height and the more photo-synthesis partitioned to kernels that increased their weight and thereby harvest index. This suggested that improvement of biomass yield would result in a substantial increment on grain yield that could be used in selection of genotypes for high grain yield at optimum condition. According to Kearsey and Pooni (1996), the positive correlation of these characters with grain yield resulted from the presence of strong coupling linkage of genes or the characters may

be the result of pleiotropic genes that control these characters in the same direction. They further suggested that the presence of such genes effects leads to the improvement of yield as seen in these characters. The positive and significant association of grain yield with biological yield and harvest index had been reported by Kifle et al. (2016), Kumar et al. (2016) and Ebrahimnejad and Rameeh (2016). The work of Surma et al. (2012) showed positive and significant correlation of grain yield with thousand kernel weight, hectoliter weight and starch content. In contrast to the current study result, Singh (2014) reported the presence of negative correlation between grain yield and plant height.

Grain yield was negatively and significantly correlated with grain protein content (-0.38). It also had negative and non-significant association with wet gluten content and Zeleny sedimentation value. The low yielding ability of the high protein genotypes is usually explained by the high energy needed for protein production as compared to starch production (Monaghan et al., 2001). But under ideal environment, assimilates are used more for grain yield than protein content. This indicated the importance of considering harvest index as it contributed more to the grain yield. However, different hypotheses dealing with the cause of this negative correlation have been also proposed, mainly related to genetic incompatibility (linkage, pleotropy) (Iqbal et al., 2007). Therefore, care should be given while selecting genotypes for grain yield and grain protein content. The results obtained in this study are in agreement with the findings of Surma (2012), in which grain yield was negatively correlated with protein content, wet gluten and Zeleny sedimentation value. Days to maturity had significant and negative association with number of productive tillers (-0.42 and -0.17), harvest index (-0.34 and -0.19), thousand kernel weight (-0.35 and -0.23), hectoliter weight (-0.49 and -0.27) and grain protein content (-0.30 and -0.27) both at genotypic and phenotypic levels (Table 4). The negative association of grain protein content with maturity suggested that early maturity and high protein content can be readily achieved simultaneously.

Genotypic path analysis

Biomass yield (0.85) followed by harvest index (0.70) exerted the highest positive direct effect on grain yield, while plant height had negligible positive direct effect, though it exhibited significant and positive association with grain yield (Table 5). The result indicated that the positive and significant correlation of biomass yield and harvest index with grain yield at genotypic level was due to the direct effect of these characters on grain yield. However, the positive association of plant height with grain yield was due to the indirect effect of this character on yield through other characters such as biomass yield, grain filling period and days to heading. The maximum positive genotypic direct effect of biomass yield and harvest index on grain yield was reported by many authors (Obsa, 2014; Dargicho et al., 2015; Alemu et al., 2016).

The genotypic correlation coefficients of thousand kernel weight, hectoliter weight and starch content were significant and positive with grain yield; however, these characters had low and negligible negative direct effect on grain yield. This implies that the indirect effects of these characters on grain yield through other characters could be the cause for significant and positive correlation. For instance, the indirect positive effect of thousand kernel weight via harvest index (0.27), hectoliter weight via harvest index (0.25) and starch content via biomass yield (0.29) on grain yield were high. This shows the importance of considering harvest index and biomass yield when selection of wheat genotypes for higher grain yield is desired. In agreement with the current study results, similar results were reported by Ermias (2005), Senayt (2007) and Adhiena (2015). Grain protein content exerted negative direct effect on grain yield, consequently, selection of genotypes for high performance of grain protein content might not be effective when the breeding objective is selection of genotypes for high grain yield. Singh (2014) reported negative direct effect of grain protein content on grain yield.

Conclusion

The study indicated the presence of wide genetic variation among the wheat genotypes which can be exploited to develop high yielding varieties with desirable grain quality and early maturity in the study area and similar agro-ecologies, where terminal moisture stress is the major constraint of wheat production. Moderate GCV coupled with moderate PCV (10 to 20%) was observed for grain yield and biomass yield, indicating the effectiveness of selection based on the phenotypic performance of the genotypes. High heritability (>80%) coupled with moderate genetic advance as percent of mean (10 to 20%) was observed for days to heading and days to maturity. This implies that the variation observed was mainly under genetic control and the possibility of progress from selection. In general, in the context of plant breeding, traits that exhibited good GCV, H^2 and GAM would be useful as a base for selection; hence days to heading, days to maturity, grain yield and biomass yield were identified as the major contributors. Grain yield had positive and highly significant correlation with biomass yield and harvest index, and also significantly correlated with plant height, thousand kernel weight, hectoliter weight and starch content both at genotypic and phenotypic level. This suggested that, grain yield potential can be effectively improved by obtaining maximum expression of these characters. However, grain yield had negative and significant correlation with grain protein content, and protein content exerted negative direct

Table 5. Estimates of direct (bold and diagonal) and indirect effect (off diagonal) of different traits on grain yield at genotypic level in 49 bread wheat genotypes at Laelay-Maichew in 2016.

Traits	DH	DM	GFP	PH	NT	KPS	SKPS	SL	BY	HI	TSW	HLW	GPC	WG	ZSV	SC	r_g
DH	0.088	-0.171	0.027	0.002	0.013	-0.003	0.009	0.002	0.122	-0.309	0.003	0.006	0.033	0.003	-0.005	-0.011	-0.19
DM	0.079	-0.189	0.052	0.002	0.013	-0.004	0.010	0.002	0.190	-0.241	0.003	0.005	0.049	0.002	-0.007	-0.019	-0.05
GFP	0.033	-0.140	0.071	0.002	0.006	-0.004	0.008	0.002	0.214	-0.025	0.001	0.001	0.051	0.000	-0.007	-0.023	0.19
PH	0.023	-0.067	0.025	0.006	0.006	-0.006	0.004	0.001	0.497	0.001	0.000	0.001	0.079	-0.030	-0.009	-0.019	0.51*
NT	-0.040	0.080	-0.015	-0.001	-0.030	0.002	-0.008	-0.001	-0.031	0.266	-0.003	-0.003	-0.012	0.005	0.002	0.004	0.22
KPS	0.013	-0.037	0.014	0.002	0.003	-0.022	0.016	0.002	0.178	0.004	0.001	0.001	0.049	-0.030	-0.005	-0.002	0.19
SKPS	0.035	-0.086	0.026	0.001	0.011	-0.016	0.022	0.004	0.072	-0.055	0.003	0.003	0.015	-0.006	-0.002	-0.001	0.02
SL	0.032	-0.081	0.025	0.001	0.007	-0.007	0.014	0.006	0.048	-0.150	0.000	0.002	-0.004	0.018	0.004	-0.006	-0.09
BY	0.013	-0.042	0.018	0.003	0.001	-0.005	0.002	0.000	0.857	-0.144	0.000	-0.001	0.070	-0.022	-0.008	-0.021	0.72**
HI	-0.038	0.065	-0.002	0.000	-0.011	0.000	-0.002	-0.001	-0.175	0.707	-0.003	-0.003	0.002	-0.009	0.000	-0.003	0.53**
TSW	-0.039	0.066	-0.005	0.000	-0.012	0.003	-0.007	0.000	0.055	0.274	-0.008	-0.007	0.007	0.004	0.003	-0.022	0.31*
HLW	-0.054	0.093	-0.007	-0.001	-0.011	0.002	-0.006	-0.001	0.134	0.248	-0.006	-0.009	0.024	-0.013	-0.002	-0.019	0.37*
GPC	-0.018	0.057	-0.022	-0.003	-0.002	0.007	-0.002	0.000	-0.369	-0.010	0.000	0.001	-0.163	0.075	0.023	0.040	-0.38*
WG	0.003	-0.003	0.000	-0.002	-0.002	0.007	-0.002	0.001	-0.202	-0.067	0.000	0.001	-0.132	0.093	0.021	0.014	-0.27
ZSV	-0.015	0.046	-0.018	-0.002	-0.002	0.004	-0.001	0.001	-0.236	0.003	-0.001	0.001	-0.130	0.067	0.029	0.027	-0.23
SC	0.016	-0.060	0.027	0.002	0.002	-0.001	0.000	0.001	0.293	0.035	-0.003	-0.003	0.108	-0.021	-0.013	-0.061	0.32*

Residual effect= 0.077. DH = Days to heading, DM = days to maturity, GFP = grain filling period, NT = number of productive tillers per plant, PH = plant height, SL = spike length, SKPS = number of spike lets per spike, KPS = number of kernels per spike, BY = biomass yield , HI = harvest index, TKW = thousand kernel weight, HLW = hectoliter weight, GPC = grain protein content, WG = wet gluten, ZSV = zeleney sedimentation value, SC = starch content and r_g= genotypic coefficient of correlation.

effect. This implies simultaneous improvement of these two characters is difficult, thus care should be given during selection of these two traits. The highest positive direct effect on grain yield was exerted by biomass yield followed by harvest index both. Therefore, selection for high mean values of biomass yield and harvest index could be considered as the simultaneous selection of genotypes for high gain yield.

Generally, it is recommended to further evaluate high yielding genotypes with high grain protein content and early maturing once more at similar agro-ecologies to develop varieties. Beside this, genetic information is limited for grain quality characteristics in bread wheat genotypes in the country (Ethiopia). Hence, due attention should be given to grain quality and yield performance of bread wheat genotypes to exploit genetic potential of the crop via selection or hybridization.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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Abbreviations

DH, Days to heading; **DM,** days to maturity; **GFP,** grain filling period; **PH,** plant height; **NT,** number of productive tillers per plant; **KPS,** number of kernels per spike; **SPKS,** number of spikelets per spike; **SL,** spike length; **BY,** biomass yield; **GY,** grain yield; **HI,** harvest index; **TKW,** thousand kernel weight; **HLW,** hectoliter weight; **GPC,** grain protein content; **WG,** wet gluten; **ZSV,** zeleney sedimentation value; **SC,** starch content;

ETBW, Ethiopian bread wheat; **σ^2g,** genetic variance; **GCV,** genetic coefficient of variation; **GAM,** genetic advance as percent of mean; **GA,** genetic advance; **H^2,** broad sense heritability; **PCV,** phenotypic coefficient of variation.

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Appendix Table 1. Mean values of 17 traits of 49 bread wheat genotypes tested at Axum area in 2016.

Name	DH	DM	GFP	PH	NT	KPS	SKPS	SL	BY	GY	HI	TSW	HLW	GPC	WG	ZSV	SC
ETBW8484	57.33	101.7	44.33	82.40	1.86	39.20	15.5	7.80	9.67	4.16	44.22	33.73	79.33	12.93	28.30	34.95	63.30
ETBW8486	55.33	100.0	44.67	77.30	1.84	47.27	16.0	8.20	11.00	4.56	41.64	35.80	79.27	14.30	31.93	51.93	62.73
ETBW9019	57.33	98.3	41.00	73.77	2.60	48.37	15.2	8.00	8.33	3.84	48.15	35.23	79.13	13.57	30.57	49.33	63.20
ETBW9026	51.67	93.7	42.00	84.53	2.01	43.10	14.9	8.47	9.50	4.49	47.36	38.67	81.60	13.17	29.83	48.87	63.43
ETBW9027	52.67	94.7	42.00	74.93	1.89	41.33	15.3	8.10	10.00	4.35	43.54	37.07	81.40	14.00	32.63	50.63	63.67
ETBW9028	65.67	112.3	46.67	83.37	1.79	57.23	18.5	8.70	9.33	3.71	39.18	29.70	76.27	13.30	30.70	48.80	63.10
ETBW9029	51.67	92.3	40.67	75.40	2.02	48.83	16.5	8.47	9.50	4.24	44.93	36.30	80.67	14.03	31.67	51.50	63.23
ETBW9033	53.00	96.7	43.67	81.67	2.19	54.10	16.9	9.10	11.00	4.09	37.33	38.23	80.10	13.87	31.33	49.60	63.37
ETBW9034	52.33	90.7	38.33	79.53	1.76	49.93	15.6	8.00	8.83	4.15	48.00	34.00	79.30	14.33	31.80	50.63	62.13
ETBW9040	54.33	94.3	40.00	74.17	1.53	51.37	16.6	8.27	8.50	3.26	38.19	29.57	77.93	14.37	30.50	50.60	61.73
ETBW9042	52.67	94.7	42.00	80.37	2.07	50.77	16.3	8.40	9.00	3.68	42.55	33.93	77.83	15.30	33.90	50.03	61.13
ETBW8489	53.67	98.3	44.67	69.47	1.86	36.47	15.0	6.93	5.50	2.59	47.59	35.60	79.20	15.43	33.53	51.33	62.33
ETBW8492	54.67	100.3	46.33	82.87	2.38	47.07	15.4	8.47	9.33	4.19	44.96	39.50	79.70	13.57	30.87	46.60	62.13
ETBW9015	58.33	98.7	40.33	86.53	1.74	51.43	15.8	7.10	10.33	4.46	43.19	30.90	78.20	13.00	27.87	44.40	62.77
ETBW9016	59.33	105.0	45.67	88.13	2.13	50.70	16.7	8.27	13.00	5.44	41.82	33.10	76.90	13.30	30.40	44.37	63.67
ETBW9017	62.33	104.7	42.33	85.10	1.58	43.23	16.1	8.57	9.33	3.64	38.90	30.33	76.17	14.57	33.90	51.70	62.57
ETBW9018	59.67	102.3	42.67	77.43	1.86	51.30	16.6	8.10	8.67	3.64	42.11	30.93	77.20	14.70	31.40	51.07	61.37
ETBW9041	59.33	99.3	40.00	78.03	1.60	54.53	17.7	8.57	8.00	3.82	48.08	29.63	77.13	14.53	31.63	50.50	61.57
ETBW9051	61.67	110.3	48.67	91.83	2.17	51.20	16.8	7.63	10.33	4.36	42.25	31.70	77.03	12.97	31.47	47.45	64.27
ETBW8471	59.33	100.7	41.33	75.63	1.56	49.07	16.7	8.30	8.75	2.43	27.78	28.50	76.50	13.93	30.47	45.30	61.30
ETBW8472	64.33	114.0	49.67	89.63	1.76	41.93	15.5	9.23	9.00	3.46	38.40	31.53	75.30	13.53	30.97	48.87	62.93
ETBW8423	57.00	101.3	44.33	73.43	1.95	45.47	16.5	8.27	9.33	3.85	41.30	30.97	77.40	14.53	33.90	51.93	62.17
ETBW8474	54.00	99.3	45.33	81.80	1.71	42.93	16.4	8.37	9.83	4.21	43.11	37.90	81.10	14.70	33.03	51.43	62.53
ETBW8475	53.67	112.3	58.67	81.53	1.68	49.60	16.5	8.53	11.00	4.64	42.19	33.80	81.30	13.10	31.53	47.30	63.80
ETBW8476	63.00	110.3	47.33	78.27	1.85	42.50	14.7	7.63	10.67	4.42	41.70	33.00	79.60	12.70	29.43	44.57	63.73
ETBW8477	60.67	106.7	46.00	86.07	1.95	50.57	15.9	7.80	10.00	4.43	44.55	33.67	79.33	12.23	27.50	35.90	63.63
ETBW8478	61.67	107.3	45.67	90.43	1.81	50.97	16.4	8.20	9.67	4.04	41.65	35.83	78.27	13.70	30.30	49.43	62.77
ETBW8479	52.00	92.7	40.67	82.07	2.07	36.20	12.8	7.53	8.67	3.75	42.94	37.63	77.87	14.77	35.40	52.40	62.90
ETBW8480	56.67	97.3	40.67	89.43	1.96	41.13	15.7	7.87	11.00	5.37	49.68	36.47	80.13	13.53	28.20	49.97	62.47
ETBW8481	55.67	105.3	49.67	86.37	2.02	59.50	17.6	9.00	8.67	4.47	51.55	41.90	80.80	12.80	30.30	44.50	65.03
ETBW6861	59.33	99.3	40.00	79.60	2.38	52.13	16.6	8.00	9.00	3.84	43.18	32.60	77.90	13.63	29.40	49.87	62.07
ETBW8506	63.00	108.7	45.67	90.93	1.71	45.63	16.6	8.00	10.67	4.12	38.53	32.33	78.37	13.20	31.83	46.83	63.63
ETBW8507	49.33	87.0	37.67	77.97	2.52	36.93	14.0	8.07	9.50	4.21	44.37	35.40	81.00	14.67	34.83	52.03	63.03
ETBW7120	60.67	104.3	43.67	72.90	1.94	46.03	15.5	8.60	8.33	3.12	37.43	28.97	75.90	14.33	33.70	51.00	62.67
ETBW8508	54.00	93.7	39.67	69.03	2.04	37.47	14.1	7.43	7.33	3.54	48.15	33.50	77.73	14.00	31.80	50.27	63.13
ETBW7213	53.00	94.7	41.67	82.33	2.18	43.33	15.2	8.47	10.33	4.38	42.37	40.10	81.50	14.20	33.73	53.13	63.20

Appendix Table 1. Contd.

ETBW8509	59.33	106.7	47.33	80.83	1.62	46.57	18.6	9.60	7.00	3.28	46.92	34.57	76.60	13.90	32.20	50.27	63.77
ETBW7038	55.00	98.0	43.00	66.87	2.51	39.07	16.0	8.33	8.00	3.23	40.68	35.13	81.27	15.40	36.47	52.47	62.50
ETBW8510	72.67	118.0	44.67	82.07	1.66	51.80	18.7	9.33	10.00	3.83	38.49	36.97	79.40	13.93	34.67	50.37	64.03
ETBW8511	64.67	113.0	51.00	82.20	1.69	53.83	18.7	8.83	9.67	4.51	46.75	29.67	78.37	14.07	33.87	49.47	63.20
ETBW7147	49.00	88.0	39.00	74.43	2.29	49.03	16.0	8.13	7.67	3.70	47.61	37.07	79.83	14.00	31.07	51.03	62.17
ETBW8512	56.33	100.0	43.67	76.73	1.93	48.07	17.1	8.80	9.67	4.24	44.15	32.87	80.67	13.10	28.20	43.63	63.53
ETBW7871	66.33	114.7	48.33	82.40	1.87	44.33	17.7	8.97	9.50	4.31	45.46	27.20	73.95	15.17	36.10	51.20	61.53
ETBW8513	73.33	118.0	44.67	77.63	1.55	43.90	16.3	9.07	9.67	3.79	38.93	34.90	74.77	13.77	32.93	47.87	63.67
ETBW6940	52.67	94.0	41.33	82.20	1.69	46.53	14.8	7.47	10.00	4.52	45.21	37.70	80.70	13.53	32.20	47.13	64.50
Kakaba	57.67	101.3	43.67	81.60	1.62	47.10	17.2	8.67	9.00	3.57	39.52	31.23	78.53	12.60	27.23	43.23	63.33
Shorima	61.00	108.0	47.00	78.13	2.33	42.03	14.8	8.13	8.67	4.38	51.27	36.57	79.60	13.57	31.57	46.60	62.93
Ogolcho	72.67	117.0	44.33	78.80	1.60	40.60	14.9	8.50	9.33	2.37	26.35	32.40	77.60	13.57	32.30	47.90	64.07
king bird	59.33	104.7	45.33	81.53	2.04	49.80	16.6	8.17	10.00	4.38	43.85	32.20	79.23	11.93	27.77	34.35	64.70
Mean	58.17	102.1	44.02	80.40	1.93	46.8	16.15	8.29	9.37	3.98	42.82	34.0	78.7	13.8	31.6	48.3	62.99
CV(%)	1.65	2.79	5.48	4.83	20.1	10.1	5.78	5.86	11.69	12.6	13.90	7.21	2.01	4.99	5.89	6.93	1.03
LSD at 1%	2.13	6.19	4.93	8.49	0.81	10.2	1.95	1.06	2.41	1.07	12.78	5.11	3.23	1.45	3.96	7.40	1.38

DH=Days to heading, DM = days to maturity, GFP = grain filling period, NT = number of productive tillers per plant, PH = plant height, SL= spike length, SKPS = number of spike lets per spike, KPS = number of kernels per spike, BY = biomass yield, GY = grain yield, HI = harvest index, TKW = thousand kernel weight, HLW = hectoliter weight, GPC = grain protein content, WG = wet gluten content, ZSV = zeleny sedimentation value and SC = starch content.

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Combining ability of tropical early maize (*Zea mays* L.) inbred lines for grain yield and resistance to maize streak virus disease

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Maize is an important cereal crop in sub-Saharan Africa but production is adversely affected by maize streak virus disease (MSVD). In Ghana, re-occurrence of the disease has been reported in several regions, therefore, necessitating the development of resistant hybrids as the most sustainable and economical option. The objectives of the study were to identify parents and hybrids that combine MSVD resistance with high yield and determine the influence of maternal effect on the inheritance of MSVD resistance. To achieve these, five parental inbred lines namely: TZEI-4, TZEI-7, TZEI-22, TZEI-31 and TZEI-157 were crossed in a full diallel mating design during the major season of 2015. The resulting F1 hybrids were evaluated under natural and artificial infestations during the minor and major seasons of 2015/2016 using 9 x 3 alpha-lattice design with three replications. General combining ability (GCA) and specific combining ability (SCA) mean squares were significant for MSVD severity mean score and only SCA for grain yield. Additive gene effect was preponderant for MSVD severity mean score, whereas grain yield was influenced by non-additive gene effect. Maternal effect had no significant contribution to the inheritance of MSVD resistance. GCA by environment and SCA by environment mean squares were significant for MSVD severity mean score. GCA effects revealed that inbreds TZEI-7 and TZEI-22 were resistant to MSVD. They could be good combiners for grain yield in addition to TZEI-31 and TZEI-157. Hybrids TZEI-4*TZEI-22 and TZEI-4*TZEI-31 showed resistance to MSVD as revealed by their SCA effects and heterotic values. TZEI-7*TZEI-157, TZEI-31*TZEI-157, TZEI-22*TZEI-157 and TZEI-4*TZEI-22 had positive and significant SCA effect, mid-parent heterosis and high parent heterosis for grain yield. Promising hybrids TZEI-4*TZEI-22, TZEI-22*TZEI-157, TZEI-7*TZEI-157 and TZEI-31*TZEI-157 identified in this study should be further tested in multi-locations across Ghana to determine their stability and adaptability.

Key words: Maize streak virus disease, grain yield, resistance, full diallel, general combining ability, specific combining ability.

INTRODUCTION

Worldwide, maize (*Zea mays* L.) ranks first in production with over one billion tonnes produced in 2014 followed by rice (741 million tonnes) and wheat (729 million tonnes), although the latter ranks first in terms of harvestable area (FAOSTAT, 2015). It is distributed worldwide and serves as a staple crop to most sub-Saharan African countries, providing food and employment to a larger percentage of the entire populace (Magenya et al., 2009).

In Ghana, maize is the second most significant food crop next to cassava and it is produced in all the geographical areas with its production in the transition zone being the highest (MoFA, 2011). FAOSTAT (2015) report indicated a significant reduction in maize produced throughout the country from 1,949,897 tonnes in 2012 to 1,762,000 tonnes in 2014. This reduction has been attributed to frequent biotic and abiotic stresses including pest and disease outbreak, reduced soil fertility and drought (Cairns et al., 2012).

Maize streak virus disease (MSVD) is caused by maize streak virus (MSV) obligately transmitted by leafhoppers in the genus *Cicadulina* (Storey, 1925). It is a major foliar disease that affects maize throughout the sub-Saharan Africa (Pingali and Pandey, 2001) and its prevalence on farmers' fields has been reported in several regions of Ghana (Oppong et al., 2015). Amongst the diseases that cause economic damage to maize in the world, MSVD ranks third following northern leaf blight and grey leaf spot, besides it has remained the most severe viral disease of maize in Africa resulting in the loss of returns, which ranges from US $ 120 to 480 million yearly (Martin and Shepherd, 2009). With effective MSVD control, no less than half of this loss can be avoided (Martin and Shepherd, 2009). The disease can cause up to 100% yield loss in susceptible varieties under field conditions (Magenya et al., 2008). However, reduction in growth and yield are directly dependent on factors such as time and stage of infection and also varies with the level of resistance (Bua and Chelimo, 2010).

MSVD symptoms are characterized by broken to nearly unbroken chlorotic bands or stripes centered initially on the tertiary leaf veins and these later develop into rectangular tan-coloured lesions that run parallel with leaf veins. As the disease spreads, the lesions merge resulting in blighting of the whole leaf (Agrios, 2005). The density of striping depends primarily on the resistance of the genotypes. In highly susceptible maize plants, the entire leaf lamina shows a severe, uniform white chlorosis which may progress gradually into death of cells and tissues of the plants and afterwards die back, especially when the plants are infested at the seedling stage (Rossel and Thottapilly, 1985). Severe chlorosis in susceptible maize plants leads to stunted growth, scanty ear development, reduced seed setting and ultimately huge yield losses or occurrence of premature death (Mawere et al., 2006; Monjane et al., 2011).

Eleven strains of MSV have been identified and are designated MSV-A to MSV-K. MSV-A strain has been identified to be the most virulent and can cause significant MSVD while others attack cereals such as barley, wheat, oats, rye and millet but not maize (Martin et al., 2001; Shepherd et al., 2010). Oppong et al. (2015) reported that MSV-A1 variant was predominant in the transition and forest zones of Ghana, and it exhibits an increased level of pathogenicity than the other MSV-A variants which are MSV-A2, MSV-A3, MSV-A4 and MSV-A6 (Martin et al., 2001). The incidence and severity of MSVD can be reduced by chemical control of leafhoppers and cultural practices such as crop rotation, irrigation, inter-cropping, application of appropriate fertilizer rate and plant density manipulation but the most economically sustainable option is provided by using disease resistant varieties (Martin and Shepherd, 2009).

Despite the successes achieved in breeding for varieties with MSVD resistance, the prevalence of MSVD continues to occur in Africa, causing huge losses in yield due to the erratic changes in climate (Legréve and Duveiller, 2010) which to some extent, makes the epidemiology of the disease complex (Martin and Shepherd, 2009). Commercial varieties in Ghana, which had some degree of resistance to MSVD, have become susceptible over the years. Therefore, it is imperative to identify high-yielding, stable and novel genotypes that can resist or tolerate MSVD outbreak enhanced by drought or erratic rainfall resulting from climate change in the tropical environments.

Therefore, the objectives of the study were to identify maize genotypes that combine high yield with MSVD resistance for sustainable production and determine the effect of maternal inheritance on MSVD resistance.

MATERIALS AND METHODS

Experimental materials

Five parental inbred lines tolerant to MSVD developed at International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria and two commercial varieties (Omankwa and Aburohemaa) developed at Council for Scientific Industrial Research-Crops Research Institute (CSIR-CRI), Fumesua, Ghana were obtained for the study (Table 1).

Description of sites, experimental design and management

A crossing block was established for the five inbred lines using Full Diallel mating design at the Finatrade Farm, Department of Animal Science, Faculty of Agriculture, Kwame Nkrumah University of Science and Technology (6° 41^1N; 1° 33^1 W), Kumasi, Ghana from April to July, 2015. It falls within the semi-deciduous rain forest zone and is characterized by a bimodal rainfall pattern, from March to July and then from September to December, with an average yearly precipitation of 1500 mm. The soil type is haplic alisols (Jones et al., 2013).

An evaluation trial was carried out at Wenchi (7.7333N; 2.1W), Ghana from October, 2015 to January, 2016. Wenchi is known to be a hot spot for MSV-A1 strain, the most virulent strain of MSV especially in the minor season (Oppong et al., 2015).

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Table 1. Characteristics of maize genotypes selected for the study.

Genotypes	Pedigree	Maturity	Colour	Source
TZEI-4	TZE-W Pop x 1368 STR S7 Inb. 6	Early	White	IITA
TZEI-7	WEC STR S7 Inbred 12	Early	White	IITA
TZEI-22	WEC STR S7 Inbred 9	Early	White	IITA
TZEI-31	TZE-W Pop x LD S6 Inbred 4	Early	White	IITA
TZEI-157	TZE-Y Pop STR Co S6 Inbred 102-1-2	Early	White	IITA
Omankwa	TZE-W POP STR QPM C4	Early	White	CRI, Fumesua
Aburohemaa	EVDT-Waa STR QPM CO	Early	White	CRI, Fumesua

The evaluation site lies in the heart of the Transition zone of Ghana, characterized by two seasons of rainfall with the major season starting from March and ending in July while the minor season begins from September and ends in November or December. The soil is sandy loam

The experimental field was sprayed with rid-out (glyphosate, 360 g/l) at 5.0 l/ha before ploughing and harrowing were done. The 27 genotypes including the checks (Omankwa and Aburohemaa) were planted in a 9 x 3 alpha-lattice design with three replications. A plot consisted of two-rows of 5 m length each. The rows were spaced 75 cm apart while hills were spaced 40 cm apart. Three seeds were sown per hill and later thinned to two plants per hill at three weeks after planting (WAP). Hence, the planting density was approximately 66,667 plants/ha. Recommended crop management practices were applied. Fertilizer equivalent to 90:0:40 kg/ha of N-P_2O_5-K_2O (26:0:4) and sulphate of ammonia fertilizers were applied at two weeks after planting and at ear emergence respectively. Post emergence weeds were controlled with the application of caliherb (2,4-dichlorophenoxy acetic acid, 360g/l) at 4.5 l/ha and manual weeding when necessary.

Artificial infestation of maize genotypes with maize streak virus

Non-viruliferous leafhoppers, *Cicadulina mbila* Naudé (Hemiptera: Cicadellidae) were collected from maize evaluation fields with the use of a pooter and were reared on pearl millet (*Pennisetum americanum* L.) in insect proof cages made of galvanized metal with a wooden base (Dimension = 0.9 x 0.9 x 2 m) at the entomology section of the CSIR-CR1, Kwadaso Station. They had an acquisition access period of 48 h from maize plants severely infected with MSV. The 27 genotypes planted in cups filled with loamy soil were infested at two-leaf stage as described by Bosque-Pérez and Alam (1992) but modified. The modification was done by placing the maize seedlings in insect proof cages and after 48 h of feeding period by the viruliferous leafhoppers, they were transplanted nine days after planting after infestation with MSV to the field which has been ploughed, harrowed and laid out using 9 x 3 alpha-lattice design with three replications.

Data collected

Data such as anthesis-silking interval (ASI), plant height (PLHT), total leaf count (TLC), ear leaf area (ELA), plant aspect (PASP), ear aspect (EASP) and 100-grain weight (HGW) were recorded but only maize streak virus disease (MSVD) severity mean score and grain yield are reported. Grain yield (t/ha) was estimated from ear weight per plot, assuming a shelling percentage of 80% and then adjusted to 12.5% moisture content. Plants in a plot were visually scored for MSVD at 3, 6 and 9 WAP according to Beyene et al. (2012) scale; 1 = no symptoms on leaves, 2 = light disease symptoms on 20 to 40% leaf area, 3 = moderate symptoms on 40 to 60% leaf area, 4 = severe symptoms on 60% of leaf area, 5 = severe symptoms on 75% or more of the leaf area.

Statistical analysis

Analyses of variances (ANOVA) were performed separately on MSVD severity mean score and grain yield from the natural and artificial infestations and then combined ANOVA across environments using PROC GLM in statistical analysis system (SAS, 2003) software version 9.1. Genotypes were considered as fixed effect while environments, replications and blocks within replications as random effects. Least significant difference (LSD) was used to determine the significant differences amongst the least square means of the genotypes at the probability level of 0.05. MSVD severity mean score was square root ($\sqrt{x}$) transformed before performing the analysis, but the original value was reported after back-transformation.

The GCA effects of the parents and SCA effects of the F1 hybrids as well as their reciprocal effects under each and across environments for MSVD severity mean score and grain yield were estimated without the checks by following Griffing's Method 1, Model I (fixed effects) Griffing (1956) using DIALLEL-SAS program developed by Zhang et al. (2005) adapted to SAS software version 9.1. Effects of GCA, SCA and reciprocal were computed from the mean values adjusted for the block effects under each environment and across environments. T-test was used to detect the significance of GCA, SCA and reciprocal effects. Standard errors were estimated as square root of the GCA, SCA and reciprocal variances (Griffing, 1956).

The least square means for grain yield were used to estimate heterosis in F1 over mid-parent and high parent according to Rai (1979).

Mid-parent heterosis (MPH) = $\frac{\mathrm{F1-MP}}{\mathrm{MP}} \times 100$, MP = $\frac{\mathrm{P1+P2}}{2}$

High parent heterosis (HPH) = $\frac{\mathrm{F1-HP}}{\mathrm{HP}} \times 100$

"T" test was then performed to know whether the F1 hybrid means were significantly different from the mid-parent and high parent means as described by Wynne et al. (1970).

"t" for MPH = $\frac{\mathrm{F1-MP}}{\sqrt{3}/2\mathrm{r(EMS)}}$

"t" for HPH = $\frac{\mathrm{F1-HP}}{\sqrt{2}/\mathrm{r(EMS)}}$

where: F1 = mean of the hybrid, MP (mid-parent) = average of the two inbred parents, P1 and P2 = mean of the inbred parents, HP =

Table 2. Mean squares from combined ANOVA of 5*5 diallel analysis for maize streak disease virus severity mean score and grain yield across infestations.

Sources of variation	df	Across	
		MSVD severity	Grain yield
Env	1	3.53***	84.83***
Genotype	24	0.69***	12.58***
GCA	4	2.49***	1.67
SCA	10	0.60***	29.83***
Reciprocal	10	0.12	1.07
Genotype*Env	24	0.30***	2.11
GCA*Env	4	0.38**	1.79
SCA*Env	10	0.42***	3.53
Reciprocal*Env	10	0.13	2.20
Error	84	0.086	2.120
GCA:SCA		4.15	0.06

*Significant at p < 0.05, ** Highly significant at p < 0.01, *** Highly significant at p < 0.001; GCA: General Combining Ability, SCA: Specific Combining Ability, Env: Environment.

Table 3. Mean squares from ANOVA of 5*5 diallel analysis for maize streak disease virus severity mean score and grain yield under natural infestation and artificial infestation.

Sources of variation	df	Natural		Artificial	
		MSVD severity	Grain yield	MSVD severity	Grain yield
Genotype	24	0.20***	10.38***	0.80***	4.31*
GCA	4	0.70***	0.53	2.17***	2.93
SCA	10	0.09	25.61***	0.93***	7.75**
Reciprocal	10	0.04	1.44	0.21	1.83
Error	42	0.042	2.156	0.131	2.085
GCA:SCA		7.78	0.02	2.33	0.38

*Significant at p < 0.05, ** Highly significant at p < 0.01, *** Highly significant at p < 0.001. GCA: General Combining Ability, SCA: Specific Combining Ability.

mean of the high inbred parent, r = number of replications and EMS = error mean square.

RESULTS AND DISCUSSION

Analysis of variance for MSVD severity mean score and grain yield

The combined ANOVA across infestations revealed significant (P<0.001) effects for environment and genotype with MSVD severity mean score and grain yield (Table 2). It was observed that significant variation existed amongst the genotypes under each infestation (Table 3). These implied that the environments were distinct and sufficient genetic differences existed among the genotypes. This would therefore permit effective progress to be made from selection for MSVD resistance and yield. Genotype x environment across infestations revealed significant (p<0.001) differences for MSVD severity mean score but not for grain yield. The significance explained that the response of genotypes to MSVD differed across infestations, implying that there were probably escapes under natural infestation or virus pressure differed across environments. Consequently, higher disease pressure was observed under artificial infestation as compared to natural infestation. Bosque-Pérez et al. (1998) reported that infestation of plant with MSV at early stages leads to greater disease severity. This would then make selection of resistant genotypes difficult under only natural infestation, therefore, stressing the need to evaluate them under artificial infestation thus, enhancing stable performance and productivity of genotypes.

Partitioning the genotypes into general combining ability (GCA), specific combining ability (SCA) and reciprocal components revealed that GCA mean square was significant (P<0.001) for only MSVD severity mean

Table 4. General combining ability (GCA) effects of parental inbred lines for MSVD severity and grain yield across, and under natural and artificial infestations.

Parents	Across		Natural		Artificial	
	MSVD severity	Grain yield	MSVD severity	Grain yield	MSVD severity	Grain yield
	(1-5)	(t/ha)	(1-5)	(t/ha)	(1-5)	(t/ha)
TZEI-4	0.19***	-0.29	0.13**	-0.04	0.24***	-0.54
TZEI-7	-0.23***	0.10	-0.10*	0.11	-0.35***	0.10
TZEI-22	-0.21***	0.06	-0.19***	0.09	-0.22***	0.03
TZEI-31	0.19***	0.01	0.17**	-0.22	0.20**	0.24
TZEI-157	0.06	0.12	-0.02	0.06	0.13*	0.17
SE (gi)	0.071	0.15	0.033	0.240	0.059	0.236
SE (gi-gj)	0.112	0.24	0.053	0.379	0.093	0.373

*Significant at $p < 0.05$, **highly significant at $p < 0.01$, ***highly significant at $p < 0.001$; SE: standard error.

score across infestation and under each infestation (Tables 2 and 3). SCA mean square was significant for MSVD severity mean score and grain yield across infestations and artificial infestation while only grain yield under natural infestation (Tables 2 and 3). Significant GCA and SCA mean squares observed for MSVD severity mean score across infestations showed the relative contributions of additive and non-additive gene effects on the expression of MSVD resistance. However, grain yield was solely controlled by non-additive gene effect as revealed by its significant SCA. Significant GCA by environment and SCA by environment mean squares were detected for only MSVD severity mean score (Table 2). These indicated that the response of both parental inbred lines and hybrids to MSVD differed across environment, suggesting that selection for resistance to the disease should be done in specific target environment. Non-significant reciprocal effect observed for MSVD severity score (Tables 2 and 3) implied that maternal effect had no significant contribution to the inheritance of MSVD resistance, therefore in future maize hybrid breeding programmes targeting MSVD resistance, the choice of a maternal parent is not very important.

GCA mean squares to SCA mean squares ratios across infestation and under each infestation for MSVD severity mean score indicated that additive gene effect was preponderant in the control of MSVD resistance in the genotypes evaluated; this suggests that early generation testing may be efficient for selecting resistant genotypes. This result agrees with those of Vivek et al. (2010), Gichuru et al. (2011) and Mutengwa et al. (2012) who found out that additive gene effects were predominant in the inheritance of resistance to MSVD. High GCA mean square implied that the per se performance of the inbred lines used in this study should be a suitable pointer of the performance of their hybrids (Gethi and Smith, 2004; Badu-Apraku et al., 2011). For grain yield, the ratios for all were less than unity indicating that non-additive effect was more predominant, indicating that heterosis could be exploited from crossing the set of parental lines used in the study. It is therefore expedient to assess the parental inbred lines with different testers to be able to identify superior hybrids since the performance of the hybrids cannot be based on GCA alone (Hallauer and Miranda, 1988). This result agrees with Bhatnagar et al. (2004). In contrast, Sibiya et al. (2013) found out that additive gene effect was more predominant in controlling grain yield. Varying gene action controlling grain yield is dependent on the parents and environment under consideration (Gichuru, 2013).

General combining ability (GCA) and specific combining ability (SCA) effects for MSVD severity mean score, yield across, and under natural and artificial infestations

Studies on GCA and SCA effects are essential because they reveal the worth of genotypes in hybrid combinations (Mutengwa et al., 2012). Generally, negative GCA effects are associated with resistance and positive effects on susceptibility (Owolade et al., 2006; Bokmeyer et al., 2009). Parents TZEI-7 and TZEI-22 had significant and negative GCA effects while others had positive GCA effects on across infestations and under each infestation (Table 4). This implied that TZEI-7 and TZEI-22 were good general combiners for MSVD resistance because they contributed to resistance in the single crosses they were involved. The negative GCA effects of these inbred lines make them qualified to be used as testers in selection of MSVD resistant genotypes (Pswarayi and Vivek, 2008). Across infestations, hybrids that expressed resistance to MSVD in terms of SCA effects were TZEI-4*TZEI-31 (-0.37), TZEI-4*TZEI-22 (-0.20), TZEI-22*TZEI-4 (-0.14), TZEI-31*TZEI-4 (-0.08), TZEI-22*TZEI-157 (-0.06), TZEI-31*TZEI-22 (-0.06), TZEI-

Table 5. Specific combining ability (SCA) effects of F1 hybrids for MSVD severity and grain yield across, and under natural and artificial infestations.

F1 Hybrids	Across		Natural		Artificial	
	MSVD severity (1-5)	Grain yield (t/ha)	MSVD severity (1-5)	Grain yield (t/ha)	MSVD severity (1-5)	Grain yield (t/ha)
TZEI-4*TZEI-7	0.24*	0.45	0.12	0.71	0.36**	0.20
TZEI-4*TZEI-22	-0.20*	1.09*	0.08	1.642**	-0.47***	0.53
TZEI-4*TZEI-31	-0.37***	0.60	-0.17	0.87	-0.57***	0.34
TZEI-4*TZEI-157	0.10	2.03*	0.27	3.11*	-0.07	0.95
TZEI-7*TZEI-22	0.08	0.26	-0.11	0.29	0.27*	0.23
TZEI-7*TZEI-31	0.02	0.63	-0.08	0.88	0.12	0.38
TZEI-7*TZEI-157	0.44*	4.78***	-0.002	6.52***	0.88***	3.05*
TZEI-22*TZEI-31	0.10	0.49	0.09	0.73	0.11	0.24
TZEI-22*TZEI-157	-0.06	2.60**	-0.14	3.68**	0.03	1.51
TZEI-31*TZEI-157	0.09	3.88***	0.09	4.18**	0.08	3.58**
TZEI-7*TZEI-4	0.21	-0.11	0.11	-0.18	0.31*	-0.04
TZEI-22*TZEI-4	-0.14	0.12	0.01	-0.20	-0.29	0.44
TZEI-22*TZEI-7	0.04	0.01	0.02	0.55	0.06	-0.53
TZEI-31*TZEI-4	-0.08	-0.46	-0.09	-0.26	-0.07	-0.66
TZEI-31*TZEI-7	-0.01	-0.56	-0.10	0.19	0.08	-1.31
TZEI-31*TZEI-22	-0.06	-0.21	-0.12	-0.19	-0.01	-0.22
TZEI-157*TZEI-4	-0.01	-0.18	-0.02	-0.19	0.004	-0.17
TZEI-157*TZEI-7	0.07	0.14	-0.11	-0.07	0.25	0.36
TZEI-157*TZEI-22	0.07	0.42	-0.09	1.30	0.23	-0.46
TZEI-157*TZEI-31	0.12	-0.25	0.05	-0.38	0.19	-0.13
S.E. (sij)	0.153	0.448	0.069	0.494	0.122	0.486
S.E.(sij-sik)	0.235	0.686	0.106	0.758	0.187	0.746
S.E. (rij-rkl)	0.147	0.606	0.118	0.848	0.209	0.834

*Significant at $p < 0.05$, ** Highly Significant at $p < 0.01$, *** Highly Significant at $p < 0.001$, SE: Standard Error.

31*TZEI-7 (-0.01) and TZEI-157*TZEI-4 (0.01) but only the SCA effects of the first two were significant (Table 5). In most of these hybrids, one of the parents had corresponding negative GCA effect except for TZEI-4*TZEI-31, TZEI-31*TZEI-4 and TZEI-157*TZEI-4. Significant SCA effects reveal that the level of resistance of certain hybrids were higher or lower than expected on the basis of the GCA of the two parents involved in the cross (Falconer and Mackay, 1996) and these effects are pinpointing to dominant gene action. Despite the positive GCA effects observed for parents TZEI-4 and TZEI-31, the SCA effect observed for the resultant straight cross hybrid was negative. This could be because of the presence of quantitative trait loci (QTLs) that were too small in effect to be expressed in each of the parents but sufficient to be detected when they are combined.

Parental inbred lines TZEI-157, TZEI-7, TZEI-22 and TZEI-31 contributed 0.12, 0.10, 0.06 and 0.01 t/ha to the grain yields observed in the hybrids across infestations. One or both of the parents involved in the following crosses TZEI-7*TZEI-157, TZEI-31*TZEI-157, TZEI-22*TZEI-157, TZEI 4*TZEI-157 and TZEI-4*TZEI-22 had positive GCA effect, suggesting that favourable genes were transmitted to the progenies (Badu-Apraku and Oyekunle, 2012). This implies that these hybrids can be used as testers in subsequent maize breeding programmes.

Mid-parent heterosis (MPH) and high parent heterosis (HPH) for grain yield across natural and artificial infestations

Plant breeders exploit heterosis by crossing distantly related genotypes in order to achieve an increase in desirable traits as compared to the mid-parent or high parent values. All the hybrids showed significant and positive superiority over the mid-parent and high parent except for the non-significance of TZEI-4*TZEI-31 and TZEI-4*TZEI-157 for HPH (Table 6).

This suggests the likelihood of using these crosses for hybrid maize production. The MPH and HPH of all the

Table 6. Heterosis for grain yield in 20 F1 hybrids across, natural and artificial infestations.

F1 Hybrids	Grain Yield					
	Across		Natural		Artificial	
	MPH (%)	HPH (%)	MPH (%)	HPH (%)	MPH (%)	HPH (%)
TZEI-4*TZEI-7	126.58**	107.25*	150.24**	83.39*	100.12*	66.07
TZEI-4*TZEI-22	111.35**	99.67*	101.61**	95.66*	125.97*	89.59*
TZEI-4*TZEI-31	100.41*	76.11	105.64*	59.04	93.16	80.96
TZEI-4*TZEI-157	121.21*	71.15	137.10*	53.38	101.74	99.28
TZEI-7*TZEI-22	129.93**	99.78*	198.43***	123.17**	68.09	65.81
TZEI-7*TZEI-31	162.56**	151.18*	285.03***	255.72**	72.25	51.16
TZEI-7*TZEI-157	332.53***	259.00***	569.07***	446.42***	195.72***	147.84**
TZEI-22*TZEI-31	149.55**	108.84*	178.35***	121.37**	118.08*	93.66*
TZEI-22*TZEI-157	192.88**	117.74*	312.98***	171.54***	79.04	51.74
TZEI-31*TZEI-157	253.54***	204.52**	298.73**	206.31**	219.56***	202.87**
TZEI-7*TZEI-4	137.92**	117.62*	181.68***	107.37**	88.99*	56.83
TZEI-22*TZEI-4	136.86**	123.77**	163.32***	155.69***	97.18*	65.44
TZEI-22*TZEI-7	139.15**	107.79*	192.81***	119.56**	90.70*	88.12*
TZEI-31*TZEI-4	162.76**	130.90*	166.68***	107.98**	157.32**	141.07*
TZEI-31*TZEI-7	217.51***	203.75**	284.48***	255.04**	168.13**	135.29**
TZEI-31*TZEI-22	167.17**	123.59**	191.89***	132.88**	140.17**	113.38*
TZEI-157*TZEI-4	157.57**	99.28*	181.30**	82.84*	128.47*	125.68*
TZEI-157*TZEI-7	303.69***	235.07***	575.95***	451.82***	146.23**	106.36*
TZEI-157*TZEI-22	163.51**	95.90*	199.18**	96.86*	129.69**	94.67*
TZEI-157*TZEI-31	309.72***	252.91***	432.84***	309.79***	217.15***	200.59**

*Significant at $p < 0.05$, ** Highly Significant at $p < 0.01$, *** Highly Significant at $p < 0.001$, MPH: Mid-Parent Heterosis, HPH: High Parent Heterosis.

hybrids exceeded 100% but hybrids with exceptional heterosis were TZEI-7*TZEI-157, TZEI-157*TZEI-31, TZEI-157*TZEI-7, TZEI-31*TZEI-157 and TZEI-31*TZEI-7. Heterosis in maize for yield has been reported by several authors (Kara, 2001; Betran et al., 2003; Gissa et al., 2007; Flint-Garcia et al., 2009). The average MPH and HPH estimates for set of hybrids evaluated by Betran et al. (2003) across environments were 171 and 132%, respectively compared closely to approximate estimates of 179 and 139% observed in this study. The significant, positive and high heterosis expressed in F1 hybrids for grain yield revealed the preponderance of dominant gene action. This is buttressed by the significant SCA observed for grain yield. Hull (1945) was of the view that non-additive effects (dominance and/or epistasis) were of greater importance for the expression of heterosis and that selection should be emphasized for specific combining ability (Sprague and Tatum, 1942). According to Sprague (1983) and Hill et al. (1998), accumulation of good dominant alleles and masking of deleterious effects of recessive alleles by their dominant alleles in the F1 as well as the superiority of F1 heterozygote at a number of its loci to both the homozygous parents have brought about the heterosis. Therefore, the exploitation of heterosis for higher grain yields from these set of single cross hybrids are a breeding advantage.

Conclusion

Important genetic materials, which can be utilized for succeeding breeding programmes, were identified. Across infestations, estimates of GCA revealed that TZEI-7 and TZEI-22 were good combiners for MSVD resistance and also TZEI-7, TZEI-22, TZEI-31 and TZEI-157 can be considered for higher grain yields. TZEI-4*TZEI-22, TZEI-22*TZEI-157, TZEI-7*TZEI-157 and TZEI-31*TZEI-157 were the best performing hybrids in terms of combining resistance or tolerance with high yield based on SCA effects and heterosis. Thus, they can be further evaluated in multi-locations for possible release for commercial production by farmers. TZEI-7*TZEI-157 and TZEI-31*TZEI-157 can be further improved for resistance by using them as females in the development of three-way cross hybrids so that their potential for high yields can be fully exploited.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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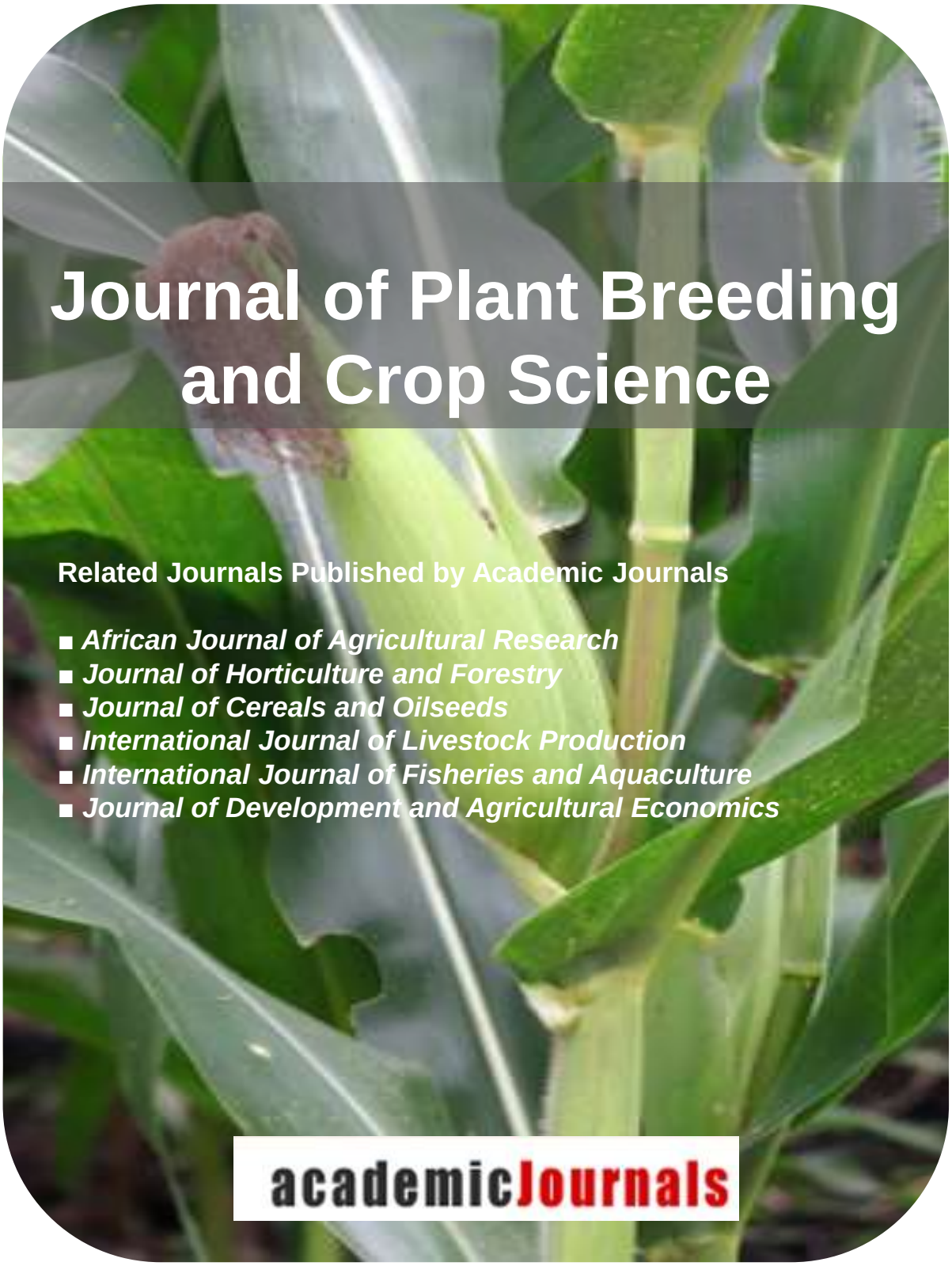

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