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Research paper

Generation mean analysis in finger millet (*Eleusine coracana* L. Gaertn)

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The choice of an efficient breeding procedure depends to a large extent on knowledge of the genetic system controlling the character to be selected. The objective of this study was to determine finger millet yield and yield components inheritance type and maternal effect existence and magnitude with analysis of generation mean. Ten generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) and reciprocals (RF_1, RF_2, RBC_1 and RBC_2) developed from improved variety "Necho" x landrace "Tikur dagusa" cross. The results showed that, the presence of genetic variation for all traits. No significant differences were found for all the characters studied between F_1, F_2, BC_1 and BC_2 with their corresponding reciprocal generations; which indicating the absence of maternal effect. The scaling test and six parameter model predominantly self-pollinated crops like finger millet additive component of gene action are more useful for breeders for successful exploitation in the selection programme, by corresponding with additive x additive type of interaction effects and complementary type of epistasis. Hence, the types of inheritance found in the studied traits were both additive and non-additive gene effects. This suggest recurrent selection breeding method at early and later generations for the possibility of developing pure line and hybrid varieties of finger millet.

Key words: *gene actions, reciprocal cross, scaling test, six generation*

INTRODUCTION

Finger millet (*Eleusine coracana* L. Gaertn) is important staple crop (Yayeh et al., 2021) grown in more than 25 countries of Africa and Asia under rain-fed conditions (http://www.cgiar.org/our-strategy/). However, it is the most neglected cereal crop grown on marginal lands under poor management condition and resulted in very low yield (Oduori, 1998; Salasya et al., 2009). Tsehaye and Fassile (2002) and Bennetzen et al. (2003) also reported that lack of improved varieties is one of the major constraints in finger millet production. This low productivity of the crop emanates due to lack of genetic improvement that hinders over all progress of the crop in developing countries; even though environmental factors also contribute to large losses in yield (Zerihun, 2009). Cereal crops covered 10,152.02 M ha out of the total grain crop area of Ethiopia. Major crops like tef, maize, sorghum and wheat took up 29.71% (3,016.063 M ha), 20.83% (2,114.88 M ha), 18.07% (1,834.651 M ha) and 16.39% (1,663.85 M ha)) of cereal crops area, respectively whereas finger millet received 4.47% (about 453.91 M ha). As to production, cereals contributed the highest (about 23,607.662 M tons) of the grain production similar as that of the area. Out of which maize, tef, sorghum and wheat made up 30.65% (7,234.96 M tons), 20.12% (4,750.66 M tons), 18.38% (4,339.134 M tons) and 17.92% (4,231.59 M tons) of the cereal production, in the same order as compared to finger millet 3.88% (about 915.315 M tons) (CSA, 2015). The survey results show finger millet area and productions are low as compared to the major cereal crops grown in Ethiopia.

According to Zerihun et al. (2010) this orphan crop play a key role in the livelihood of the resource-poor farmers and consumers in Africa, because they perform better than the major world crops under extreme soil and climate conditions prevalent in the continent. However, the productivity is low in Ethiopia (2016 kg/ha) and particularly in west Gojam zone (1661 kg/ha) (CSA, 2015) as compared to highest western Kenya (2500 kg/ha) and it is also far below as compared to a potential > 5,000 kg/ha (National Research Council, 1996; Oduori, 2008) and 7500 kg/ha (ACET and KIRDI, 2014). This evidence indicates the potentiality of the crop for improvement in yields. The gene effects controlling the quantitative traits of economically important crops nature and magnitude information are the base for any crop improvement program achievement. The performances of yield components determine the real grain yield potential of the crops; since it is a result of complex characters that controlled by many few genes. The fundamental understanding of the genetics and inheritance that underlies the yield and its component characters are greatly help a breeder in his selection work with more precision and accuracy (Deb and Khaleque, 2009; Shashikumar et al., 2010). Additionally Bhor et al. (2014) express that, the breeder basically would require information to know in yield and yield components of plants what type of gene effect exist, to enhance the productivity of the crop. The gene actions involved in the control of inheritance for yield and yield contributing characters must be considered together with suitable statistical tools to maximize the derived genetic information. Generation mean analysis has immense use to the plant breeder in deciding suitable breeding strategy for improvement of needed characters. It is simple and useful technique among other genetic analysis methods (Kearsey and Pooni, 2004; Checa et al., 2006) especially to estimate epistatic gene effects. Though finger millet is an earlier time crop which have low breeding efforts for developing potential hybrids and for genetic improvement by exploiting local germplasm as compared to other cereal crops such as wheat, barley, tef etc.,. With this consideration, the objective of this study was to determine inheritance of yield and yield components and to evaluate the presence and magnitude of any "maternal effect" in finger millet.

MATERIALS AND METHODS

Description of the study site

This experiment had two subsequent activities such as crossing of parents and field evaluation of off springs with parents. The crossing part of this experiment was done at Haramaya University greenhouse in 2012 and 2013. The field evaluation was carried out in Yilman-Densa and Mecha Districts (*Woredas*) at Adet and Koga research centers in the same order in West Gojam Zone, northwest Ethiopia in 2014/15 crop seasons.

Crossing procedures and development of generations

In this experiment the two finger millet varieties were selected on the basis of their different response to yield and adaptation; the high yielder seed parent, Necho (P1) and the low yielder and highly adapted, local *Tikur dagusa/Abate tikur* (P2). Crosses were made as follows: for direct cross-P1 x P2 and reciprocal cross-P2 x P1and the first letter of both crosses represented female parent. First filial generation (F1) and reciprocal first filial generation (RF1) of direct and reciprocal crosses were grown and self-pollinated to produce second filial generation (F2) and reciprocal second filial generation (RF2), respectively. The F1 and RF1 of crosses were back crossed to both parents using the F1and RF1 plants as female.

Table1. Geographical description of the experimental sites

Location	Elevation (masl)	Latitude	Longitude	Temperature °C Maximum	Minimum	Annual rain fall (mm)
Mecha*	1960	11°25'20" N	37°10'20" E	27.9	9.6	1557.9
Adet**	2240	11°16'19''N	37°28'38''E	26.4	10.9	1215.2

Source: WAMSC, 2014; Berhanu et al., 2014*; NSRC, 2006**

Table 2. Soil physical and chemical properties of the experimental area

Location	Soil pH	Textural class	Soil type	% O.M	% Total N	Available P (ppm)
Mecha*	5.09-5.3	Clay	Nitosol	2.34-4.44	0.18-0.24	3.54-8.7
Adet**	5.38-5.48	Clay	Luvisol	2.67-2.86	0.17-0.47	2.64-2.76

Source: Berhanu et al., 2014*; N- Nitrogen; NSRC, 2006**; O.M- Organic matter; P- Phosphorus, ppm - parts per million.

Figure 1. Finger millet emasculation and crossing with contact method

Backcrosses of F1 to high parents were back crossed one (BC1) and to low parents back cross two (BC2). The other reciprocal back cross one (RBC1) and reciprocal back cross two (RBC2) were resulted from crossing of RF1 to high parents and low parents, respectively. Hence, generally eight generations, i.e. F1, F2, RF1, RF2, BC1, BC2, RBC1 and RBC2 were developed through a stepwise crossing from January 2012 to September 2013 and then field evaluation was continued. During crossing, the two parents were planted in the green house under optimal growth conditions. Using the two parents, F1 and RF1 generation were produced from January 2012 to August 2012. The F1 and RF1 seeds were planted to produce F2 and RF2 population through selfing. Hence, the backcross population (BC1 and BC2) and reciprocal back cross population (RBC1and RBC2) were generated through crossing the F1 to P1 and P2 from January 2013 to September 2013. Seeds of direct crosses and reciprocal crosses were sown in June to July 2014 and harvested from December 2014 to January 2015. Pollination of female flowers were applied very early in the morning i.e., before 6 am after work of hand emasculation were finished in the evening. Open inflorescence of male parents were selected, cut with long stalk and brought to the emasculated female flowers. Thus, the female flower was fully tied round by the male flower and then which covered using butter paper bag with principle of contact method. The pollination takes place 2 to 5 days, until then the cut end of the male inflorescence was immersed in water and kept in a bottle (TNAU, 2008).

Experimental materials

Seeds of the ten generations such as: the two parents, Necho (P1) and *Tikur dagusa* (P2); the first and second filial generations “F1 (P1xP2) and F2 (self of F1)”, respectively; back crosses “BC1 (F1 x P1) and BC2 (F1 x P2)” and their reciprocal crosses “RF1 (P2 x P1); RF2 (self of RF1); RBC1 (RF1x P1) and RBC2 (RF1x P2)” were sown in variable rows.

Experimental design

Each generation was planted with 15 cm plant to plant and 40 cm row to row spacing in plot of 5 m length. The parents, F1 and RF1 generations were planted in a single row each, two rows each for backcross and reciprocal backcross, while each F2 and RF2 generations were grown in a plot of three rows (Akhtar and Chowdhary, 2006; Yadav and Singh, 2011).The evaluation of the trial was organized in open field condition in Randomized Complete Block Design (RCBD) with two replications during 2014/2015 crop season.

Agronomic management

The seed rate of 15 kg/ha and fertilizer rate of 100/50 kg/ha for DAP and UREA were applied in rows, respectively as cited by (Molla, 2012). The nutrient phosphorous was totally applied at basal, whereas half amount of nitrogen was applied during planting and the remaining was top dressed at tillering stage. The experimental plots become free of weeds over the growing season by applied one and two times hand hoeing and weeding, respectively. In general the land preparation and other agronomic practices were made uniformly on all plots.

Data collected

The number of plants sampled for traits in each experimental unit (plot) varied among generations depending on the expected level of heterogeneity in the generation. Accordingly, for non-segregating generations such as P1, P2, F1 and RF1 sampled 10 plants due to its homogeneity; correspondingly for segregating generations, 20 from each backcross and its reciprocals and 30 plants from each F2 and RF2 generations due to its heterogeneity (Akhtar and Chowdhary, 2006; Yadav and Singh, 2011). Data recorded was made for plant height (cm), number of tillers, number of ears, number of fingers/ear and finger length (cm) on plant basis. While, plot basis recorded for days to flowering, days to maturity, harvest index (%), thousand seed weight(g), seed yield (kg/ha) and biomass yield (kg/ha).

Data analysis

Data were subjected to statistical analysis using SAS statistical software (SAS, 2002). Mean separation was done using Duncan multiple range test to identify maternal effects using Steel et al. (1997) method by determining generation means and reciprocal cross differences. The generation means analyses and estimation of gene effects were made on six generations. The different characters data for adequacy of additive dominance model were first tested using “scaling tests (A, B, C and D)” (Mather, 1949; Hayman and Mather, 1955). Generation mean analysis was performed using the Mather and Jinks (1982) method to detect the presence of epistasis.

The A, B, C and D scaling test with six generation means:

$A = 2 B_1 – P_1 – F_1$; $B = 2 B_2 – P_2 – F_1$; $C = 4 F_2 – 2 F_1 – P_1 – P_2$; $D = 4 F_3 – 2 F_2 – P_1 – P_2$

Since A, B, C and D are different from zero make test of significance if additive-dominance model is violated or not. To do so calculate first variance this is given as:

$V_A = 4 V(B_1) + V(P_1) + V(F_1)$; $V_B = 4 V(B_2) + V(P_2) + V(F_1)$, $V_C = 16 V(F_2) + 4 V(F_1) + V(P_1) + V(P_2)$; $V_D = 16 V(F_3) + 4 V(F_2) + V(P_1) + V(P_2)$

The significance of the above parameters is tested with the help of‘t’:

S.E. (A) = $(V_A)^{1/2}$; S.E. (B) = $(V_B)^{1/2}$; S.E. (C) = $(V_C)^1/2$; S.E. (D) = $(V_D)^{1/2}$

S.E. = Standard error, V= variance

Now, the‘t’ values are calculated as follows:

t(A) = A / S.E.(A); t(B) = B / S.E.(B); t(C) = C / S.E.(C); t(D) = D / S.E.(D).

As showed by chi square ($\chi2$), the joint scaling test (Cavalli, 1952; Mather and Jinks, 1982) was extended to fit the six parameter model as outlined by Jinks and Jones (1958) to investigate the suitability of the genetic model controlling the studied traits. The simple genetic model (m, d, and h) was applied when epistasis was absent, whereas in the presence of non-allelic interaction the analysis was proceeded to estimate the inter\action types involved using the six parameters genetic model, according to Hayman (1958).

Components of generation mean:-

Six parameters model are:

m = Mean = $F_{2;}$

d = Additive effect = $B_1 – B_{2;}$

h = Dominance effect = $F_1 – 4 F_2 – (1/2) P_1 – (1/2) P_2 + 2 B_1 + 2 B_{2;}$

i = Additive x Additive type of gene interaction = $2 B_1 + 2 B_2 – 4 F_2$

j = Additive x Dominance type of gene interaction = $B_1 – (1/2) P_1 – B_2 + (1/2) P_{2;}$

l = Dominance x Dominance type of gene interaction = $P_1 + P_2 + 2 F_1 + 4 F_2 – 4 B_{2.}$

The estimates of gene effects variances were obtained as follows:

Vm = VF2; Vd = VBC1 + BC2; Vh = 4(VBC1 + VBC2) + VF1 + 16VF2 + ½ (VP1 + VP2)

Vi = 4 (BC1 + BC2) + 16V F2; Vj = 4(VBC1 + VBC2) + (VP1 + VP2)

Vl = VP1 + VP2 + 4VF1 + 16(VG2 + VBC1P1 + VBC1P2)

Where, Vm, Vd, Vh, Vi, Vj and Vl were variances of m, d, h, i, j and l, respectively. VP1, VP2, VF1, VF2, VBC1 and VBC1 were variances of the mean of these estimates that provided standard errors for testing the significance of corresponding estimates.

The six generation means data were utilized by the joint scale test (Cavalli, 1952) to estimates weighted least square value of [m], [d] and [h]. The weights are the reciprocals of the standard error of generation means and then the weighted values of [m], [d] and [h] are used to calculate the expected generation means. Then comparison between observed and expected means may then be effected by assuming the sum of squares minimized in the fitting process to be distributed as $\chi2$ with degree of freedom equal to the number of generation minus the number of parameters which have been used in the fitting process. The t-test was estimated the significance of components within each model. The type of epistasis such as: duplicate and complementary was observed when the gene effects had the opposite and same sign of significant dominance* dominance [l] and dominance [h] gene effects, respectively (Farshadfar et al., 2008; Khattab et al., 2010). Generation mean analysis and determination of components of parameters was computed using statistical program (SPAR, 2.0).

RESULTS AND DISCUSSION

Analysis of variance

Analysis of variance indicated the presence of highly significant differences ($P\leq0.01$) among generation for all traits at Adet (Table 3) and for all traits except plant height ($P\leq0.05$) at Mecha (Table 4). This finding was agreed to the outcome of Chaudhary et al., 1996; and Foroozanfar and Zeynali (2013) in bread wheat. The foregoing statement ensures the presence of high genetic potential among these generations so that generation mean analysis is proceeding as generation effects found significantly different as suggested by (Kearsey and Pooni, 1996; Dvojkovic et al., 2010).

Maternal effects

The maternal effects have a capacity to determined variation in an individual's phenotype like determined by the genotype and environment of that individual; that is, the contribution of the maternal parent to the phenotype of its offspring beyond the equal chromosomal contribution expected from each parent (Roach and Wulff, 1987). Maternal effect results in the production of difference between reciprocal crosses, which are shown between the offspring of both sexes in all the generations where they occur. In this experiment we took advantage from information based on 10 generations to estimate maternal effect. A comparison was made between the means using the Duncan multiple range test (DMRT) for contrasts F1 vs. RF1, F2 vs. RF2, BC1 vs. RBC1 and BC2 vs. RBC2. The reciprocal F1's, F2's and backcrosses for all traits were not significantly different to their main effect in both locations (Table 5 and Table 6). The absence of significant difference between the direct and reciprocal crosses indicated that genes controlling finger millet yield and yield components were all nuclear genes and that the cytoplasmic genes of the mother had no effect on the inheritance of finger millet traits such as PH, FL, NT, NF, DTF, DTM, SY, BMY, HI and TSW. These results are in resemblance to previous report on tef (Hailu and Peat, 1997) and on cowpea (Noubissie Tchiagam et al., 2011). Hence, the maternal effects were not identified in this cross; this would allow selecting parents that have higher seed yield as a female parent to develop hybrid varieties in finger millet. In contrast to the above findings, significant maternal effects were reported on rice PH, PL, TSN in panicle and TSW (Kiani et al., 2013).

Generation mean

Finger millet yield and its components mean performance of the generations are presented in Table 5 and Table 6. The results revealed that the studied materials have the genetic variability for their characters. All the traits except plant height, days to flowering, days to maturity and thousand seed weight of the F1's mean value were greater than the mid parental value. Additionally the F1's mean value was significantly above that of the F2's, except for traits days to flowering, days to maturity and thousand seed weight; whereas, the F2's mean value was better than the mid value of parental lines for the traits finger length, number of finger, days to maturity, seed yield, harvest index and thousand seed weight. The backcross to P1 were significantly different from backcross to P2 excluding thousand seed weight character at Adet (Table 5). Similarly, at Mecha the mid parent and mean of F2's value of all traits was lower than to the F1's mean value except to days to flowering, days to maturity and thousand seed weight. Backcross to P1 was significantly different from backcross to P2 except to seed yield, harvest index and thousand seed weight (Table 6).

Table 3. Analysis of variance of yield and yield contributed traits of all generations in finger millet cross at Adet

Source of variation	DF	PH cm	FL cm	NT	NF	NE	DTF	DTM	SY kg	BMY kg	HI	TSW g
Replication	1	0.55	0.41	0.98	0.2	138.28	31.25	2.45	185978.75	2830528.8	36.96	0.07
Generation	9	24.24**	7.09**	3.32**	4.71**	13.99**	7.25**	56.72**	584122.50**	241071.13**	112.80**	0.07**
Error	9	2.74	0.14	0.32	0.18	0.44	0.58	0.45	2373.57	13455.13	4.2	0.01
CV%		2.3	3.62	5.39	4.68	4.89	0.88	0.49	2.14	2.48	4.24	2.36

*, ** = 0.05 and 0.01, respectively; DF- Degree of Freedom, PH- Plant Height, FL- Finger Length, NT- Number of Tiller, NF- Number of Finger, NE- Number of Ears, DTF- Days To Flowering, DTM- Days To Maturity, SY- Seed Yield, BMY- Bio Mass Yield, HI- Harvest Index, TSW- Thousand Seed Weight

Table 4. Analysis of variance of yield and yield contributed traits in six basic generations in finger millet cross at Mecha

Source of variation	DF	PH cm	FL cm	NT	NF	NE	DTF	DTM	SY kg	BMY kg	HI	TSW g
Replication	1	25.88	0.5	0.17	0.06	1.38	5	0.8	75651.15	581746.05	6.48	0.01
Generation	9	20.48*	4.96**	5.75**	5.46**	4.79**	8.98**	38.31**	254498.40**	383926.90**	27.34**	0.08**
Error	9	4.62	0.07	0.19	0.21	0.27	0.44	0.69	5451.06	23189.83	2.11	0.01
CV%		3.32	2.59	6.68	5.77	5.11	0.72	0.63	3.69	3.8	2.92	3.31

*, ** = 0.05 and 0.01, respectively; DF- Degree of Freedom, PH- Plant Height, FL- Finger Length, NT- Number of Tiller, NF- Number of Finger, NE- Number of Ears, DTF- Days To Flowering, DTM- Days To Maturity, SY- Seed Yield, BMY- Bio Mass Yield, HI- Harvest Index, TSW- Thousand Seed Weigh

Gene action estimates

The estimated values of scale tests A, B, C, and D together with the mean (m), additive (d) and dominance (h), and their standard errors to investigated traits are presented in Table 7 and Table 8. The mean values for studied traits subjected to the individual scaling test of Mather (1949) showed that the A, B, C and D scaling test for plant height, number of ear, days to flowering and biomass yield at Adet (Table 7) and for plant height and days to flowering at Mecha (Table 8) were not significantly different from zero. In view of the advantages associated over scaling test, the adequacy of simple additive–dominance model evaluated by accommodate the data within three parameter model using joint scaling test (Cavalii, 1952).

The presence of digenic interactions can indirectly approved with significance of scaling test for the control of inheritance in the other traits. These ensured that the presence of inadequate or insufficient simple additive dominance model or three- parameter model to explain the genetic variation exist among the means of significant traits for which scaling tests was done. Hence, the values of six generations for joint scaling tests and their interaction effect (Cavalli, 1952; Mather and Jinks, 1982) used for the six parameter components of gene effects and for the expression of all the studied characters are indicated (Table 9 and Table 10). The findings of this study are in harmony with earlier and current reports of various authors (Abd El-Majeed, 2005; Hendawy et al., 2009; Mohamed and Khaled, 2013) on wheat and (Kiani et al., 2013) on rice.

Results of generation mean computed with six parameter model for both locations are indicated (Table 9 and Table 10) and estimated values of mean effects (m) were observed significance difference. At the same time significant additive, dominance and epistasis gene actions were found under the study traits on different set of parameters. The best model was selected using the non-significant Chi- square (χ^2) value and lowest standard error for all of the studied traits in both locations and shown to be the best fit of the observed to the expected generation means. The three parameters, [m], [d] and [h] for both locations, were shown to be the best fit of the observed to the expected generation means and Chi-square (x^2) values were non-significant, which indicates digenic interaction is adequate to express the variability of the trait.

In the inheritance of the traits, both types of gene actions were mainly involved, since additive and dominance main effects were observed significantly for number of tiller and days to maturity at both locations and number of finger and number of ear at Mecha indicating that both types of gene actions were mainly involved in the inheritance of these traits. This implies the improvement needs intensive selection to these traits to later generation when dominant effect is diminished (Khattab et al., 2010). The negative value of [h] detected for some studied traits showed that the parents that

Table 5. The mean, standard error and Duncan's test of main and reciprocal effect generations of finger millet at Adet

Generation	PH	FL	NT	NF	NE	DTF	DTM	SY	BMY	HI	TSW
P1	67.30±0.70^{e}	11.45±0.35^{b}	9.40±0.30^{c}	8.90±0.40^{b}	14.70±3.60^{b}	83.00±1.00^{d}	130.50±0.50^{e}	2387.35±57.10^{b}	4966.00±484.00^{a}	48.43±3.58^{b}	3.05±0.05^{b}
P2	77.75±1.05^{a}	8.70±0.40^{d}	10.98±0.03^{b}	6.45±0.55^{d}	10.20±2.20^{d}	90.50±0.50^{a}	149.00±1.00^{a}	1550.68±76.68^{e}	4305.00±395.00^{c}	38.29±0.60^{d}	3.25±0.05^{a}
F1	72.10±0.60^{bcd}	13.75±0.25^{a}	12.50±0.10^{a}	11.50±0.30^{a}	18.00±2.10^{a}	86.50±1.50^{bc}	135.00±0.00^{c}	3203.85±109.55^{a}	5188.50±418.50^{a}	61.75±3.12^{a}	3.05±0.05^{b}
F2	70.20±1.00^{cde}	10.25±0.22^{c}	9.33±0.13^{c}	9.05±0.05^{b}	12.02±2.89^{c}	86.50±1.50^{bc}	140.50±0.50^{b}	2139.30±57.00^{c}	4592.50±307.50^{b}	46.70±1.90^{bc}	3.40±0.10^{a}
BC1	68.61±1.39^{de}	9.40±0.15^{cd}	9.50±0.30^{c}	9.00±0.20^{b}	14.00±2.60^{b}	86.00±2.00^{c}	133.00±0.00^{d}	2233.83±50.63^{c}	4622.50±519.50^{b}	46.97±2.02^{bc}	2.90±0.10^{b}
BC2	75.15±0.85^{ab}	8.73±0.48^{d}	11.25±0.75^{ab}	7.84±0.16^{c}	11.25±2.25^{cd}	88.00±1.00^{b}	139.50±0.50^{b}	1844.35±131.75^{d}	4301.50±299.50^{c}	42.87±0.08^{cd}	3.00±0.00^{b}
RF1	72.75±0.75^{bc}	13.40±0.10^{a}	12.40±0.30^{a}	11.4±0.40^{a}	17.65±2.65^{a}	86.50±0.50^{bc}	135.50±0.50^{c}	3178.30±124.30^{a}	5220.00±294.00^{a}	60.95±1.05^{a}	3.05±0.15^{b}
RF2	70.18±1.28^{cde}	10.25±0.12^{c}	9.30±0.34^{c}	9.00±0.00^{b}	12.00±2.50^{c}	86.50±1.50^{bc}	140.00±1.00^{b}	2127.40±107.10^{c}	4632.50±354.50^{b}	46.02±1.22^{bc}	3.40±0.00^{a}
RBC1	68.60±1.80^{de}	9.43±0.38^{cd}	9.50±0.80^{c}	8.90±0.30^{b}	13.85±3.15^{b}	86.00±2.00^{c}	133.00±0.00^{d}	2210.25±101.25^{c}	4631.50±401.50^{b}	47.88±1.98^{bc}	2.90±0.10^{b}
RBC2	75.75±1.25^{ab}	8.70±0.20^{d}	11.23±0.58^{ab}	7.85±0.15^{c}	11.69±2.36^{cd}	88.00±1.00^{b}	139.50±0.50^{b}	1849.45±148.95^{d}	4288.00±288.00^{c}	43.09±0.59^{cd}	3.00±0.00^{b}

Means followed by the same letters in a column are not significantly different at the 5% level of probability according to Duncan's multiple range tests. PH- Plant Height, FL- Finger Length, NT- Number of Tiller, NF- Number of Finger, NE- Number of Ears, DTF- Days To Flowering, DTM- Days To Maturity, SY- Seed Yield, BMY- Bio Mass Yield, HI- Harvest Index, TSW- Thousand Seed Weight, P1-Parent one, P2-Parent two, F1-First filial, F2- Second filial, BC1- Backcross one, BC2- Backcross two, RF1- Reciprocal First filial, RF2-Reciprocal Second filial, RBC1- Reciprocal Backcross one, RBC2- Reciprocal Back cross two

Table 6. The Mean, Standard error and Duncan's test of main and reciprocal effect generations of finger millet at Mecha

Generation	PH	FL	NT	NF	NE	DTF	DTM	SY	BMY	HI	TSW
P1	59.45±1.15^{d}	10.75±0.45^{b}	6.70±0.40^{c}	8.80±0.80^{b}	10.70±0.10^{b}	89.50±0.50^{d}	121.50±0.50^{d}	2169.60±29.40^{b}	4296.00±104.00^{ab}	50.52±0.54^{b}	3.20±0.20^{bc}
P2	69.55±3.45^{a}	8.35±0.15^{e}	4.70±0.10^{d}	5.50±0.20^{e}	7.35±0.35^{d}	97.00±0.00^{a}	137.50±0.50^{a}	1506.15±17.85^{d}	3194.50±78.50^{d}	47.16±0.60^{bc}	3.50±0.10^{a}
F1	67.50±3.50^{ab}	13.10±0.10^{a}	9.00±0.20^{a}	10.40±0.20^{a}	12.30±1.00^{a}	92.00±0.00^{c}	129.00±1.00^{c}	2603.25±32.00^{a}	4634.00±246.00^{a}	56.30±2.30^{a}	2.93±0.03^{d}
F2	63.83±0.93^{bcd}	10.15±0.15^{bc}	5.30±0.30^{d}	8.30±0.10^{bc}	9.30±0.10^{c}	93.00±1.00^{c}	134.00±1.00^{b}	1881.50±11.50^{c}	4028.00±12.00b^{c}	46.68±0.12^{c}	3.38±0.03^{ab}
BC1	61.18±0.48^{cd}	9.9±0.30^{c}	7.65±0.35^{bc}	7.25±0.15^{cd}	10.48±0.18^{bc}	91.50±0.50^{c}	129.50±0.50^{c}	1921.63±130.63^{c}	3975.50±247.50^{bc}	48.32±0.28^{bc}	3.10±0.00^{cd}
BC2	66.10±0.90^{abc}	9.05±0.25^{d}	4.90±0.10^{d}	6.30±0.30^{de}	9.25±0.25^{c}	95.00±0.00^{b}	133.00±0.00^{b}	1751.00±84.30^{c}	3662.00±229.00^{c}	47.84±0.67^{bc}	3.08±0.03^{cd}
RF1	67.53±2.23^{ab}	12.95±0.35^{a}	8.90±0.40^{a}	10.25±0.25^{a}	12.50±0.50^{a}	93.00±0.00^{c}	129.50±0.50^{c}	2590.00±40.00^{a}	4605.00±261.0^{a}	56.38±2.33^{a}	2.90±0.00^{d}
RF2	63.50±0.50^{bcd}	10.20±0.10^{bc}	5.40±0.20^{d}	8.40±0.10^{b}	9.25±0.25^{c}	93.00±1.00^{c}	134.50±0.50^{b}	1891.65±13.35^{c}	4037.50±6.50^{bc}	46.85±0.25^{c}	3.40±0.00^{ab}
RBC1	62.10±0.90^{cd}	9.85±0.15^{c}	7.75±0.55^{b}	7.30±0.20^{cd}	10.50±0.30^{bc}	92.00±1.00^{c}	129.50±0.50^{c}	1926.50±153.50^{c}	3962.50±262.50^{bc}	48.57±0.67^{bc}	3.10±0.00^{cd}
RBC2	66.10±0.60^{abc}	9.08±0.08^{d}	4.93±0.08^{d}	6.33±0.08^{de}	9.30±0.50^{c}	95.00±1.00^{b}	133.00±0.00^{b}	1752.50±102.50^{c}	3675.50±258.50^{c}	47.73±0.58^{bc}	3.05±0.05^{cd}

Means followed by the same letters in a column are not significantly different at the 5% level of probability according to Duncan's multiple range tests. PH- Plant Height, FL- Finger Length, NT- Number of Tiller, NF- Number of Finger, NE- Number of Ears, DTF- Days To Flowering, DTM- Days To Maturity, SY- Seed Yield, BMY- Bio Mass Yield, HI- Harvest Index, TSW- Thousand Seed Weight, P1-Parent one, P2-Parent two, F1-First filial, F2- Second filial, BC1- Backcross one, BC2- Backcross two, RF1- Reciprocal First filial, RF2-Reciprocal Second filial, RBC1- Reciprocal Backcross one, RBC2- Reciprocal Back cross two

Table 7. Estimates of the gene effect using scaling test for various characters in finger millet cross at Adet

Parameter	Plant height	Finger length	Number of tiller	Number of finger	Number of ear	Days to flowering
A	-0.013±0.02^{ns}	-0.23±0.024*	-0.104±0.048*	-0.092±0.027*	-0.124±0.209^{ns}	0.013±0.021^{ns}
B	0.004±0.01^{ns}	-0.181±0.05*	-0.032 ± 0.048^{ns}	-0.075±0.037*	-0.152±0.182^{ns}	-0.005±0.011^{ns}
C	-0.049±0.029^{ns}	-0.215±0.035*	-0.297±0.045*	-0.051±0.043^{ns}	-0.354±0.406^{ns}	-0.002±0.032^{ns}
D	-0.026±0.032^{ns}	0.021±0.037^{ns}	-0.068±0.048^{ns}	0.138±0.038*	-0.015±0.430^{ns}	-0.002±0.034^{ns}

Jinks and Jones (1958) test

Parameter	Plant height	Finger length	Number of tiller	Number of finger	Number of ear	Days to flowering
M	1.826±0.036*	1.237±0.059*	0.887±0.078*	1.049±0.031*	1.034±0.436*	1.933±0.037*
[d]	-0.031±0.004*	0.054±0.01*	-0.031±0.006*	0.062±0.018*	0.072±0.067^{ns}	-0.019±0.003*
[h]	0.068±0.087^{ns}	-0.675±0.166*	0.267±0.215^{ns}	-0.234±0.091*	0.043±1.023^{ns}	0.026±0.090^{ns}

Continued Table 5.

Parameter	Days to maturity	Seed yield	Biomass yield	Harvest index	1000 seed weight
A	0.002±0.002^{ns}	-0.186±0.040*	-0.083±0.099^{ns}	-0.130±0.056*	-0.033±0.025^{ns}
B	-0.014±0.005*	-0.166±0.071*	-0.081±0.078^{ns}	-0.107±0.014*	-0.031±0.012*
C	0.041±0.013*	-0.259±0.083*	-0.110±0.143^{ns}	-0.169±0.060*	0.123±0.030*
D	0.006±0.014^{ns}	0.092±0.084^{ns}	-0.004±0.144^{ns}	0.070±0.059^{ns}	0.051±0.023*

Jinks and Jones (1958) test

Parameter	Days to maturity	Seed yield	Biomass yield	Harvest index	1000 seed weight
M	2.201±0.013*	3.377±0.103*	3.717±0.161*	1.712±0.065*	0.806±0.030*
[d]	-0.029±0.002*	0.094±0.012*	0.031±0.029^{ns}	0.049±0.016*	-0.010±0.004*
[h]	-0.134±0.027*	-0.316 ± 0.266^{ns}	-0.220±0.404^{ns}	-0.220±0.168^{ns}	-0.450±0.079*

* - Significant (if the value of parameter divided by its standard error exceeds 1.96)

Table 8. Estimates of scaling tests for various characters in finger millet cross at Mecha

Parameter	Plant height	Finger length	Number oftiller	Number of finger	Number of ear	Days to flowering
A	-0.029±0.02^{ns}	-0.144±0.023*	-0.013± 0.057^{ns}	-0.214±0.043*	-0.072± 0.028*	0.007±0.010^{ns}
B	-0.030±0.029^{ns}	-0.116±0.017*	-0.214±0.020*	-0.143±0.030*	-0.024 ± 0.041^{ns}	0.005±0.005^{ns}
C	-0.053±0.049^{ns}	-0.150±0.030*	-0.446±0.091*	-0.042 ± 0.045^{ns}	-0.185±0.057*	0.008±0.019^{ns}
D	-0.006±0.035^{ns}	0.054±0.032^{ns}	-0.044±0.095^{ns}	0.134±0.039*	0.036±0.042^{ns}	-0.002±0.021^{ns}

Jinks and Jones (1958) test

Parameter	Plant height	Finger length	Numberof tiller	Number of finger	Number of ear	Days to flowering
M	1.821±0.028*	1.130±0.034*	0.602±0.098*	1.216±0.038*	0.905±0.049*	1.970±0.021*
[d]	-0.033±0.011*	0.050±0.009*	0.065±0.012*	0.089±0.019*	0.073±0.009*	-0.017±0.001*
[h]	-0.051±0.068^{ns}	-0.351±0.086*	0.390±0.229^{ns}	-0.831±0.113*	0.213±0.128^{ns}	0.015±0.048^{ns}

Continued Table 6.

Parameter	Days to maturity	Seed yield	Biomass yield	Harvest index	1000 seed weight
A	0.029±0.004*	-0.187±0.064*	-0.101±0.063^{ns}	-0.084±0.019*	0.008±0.021^{ns}
B	-0.001 ± 0.002^{ns}	-0.108±0.047*	-0.044±0.063^{ns}	-0.063±0.021*	-0.026±0.011*
C	0.064±0.008*	-0.247±0.018*	-0.047±0.053^{ns}	-0.197±0.036*	0.101±0.025*
D	0.031±0.008*	0.035±0.011*	0.073±0.015*	-0.038±0.008*	0.007±0.025^{ns}

Jinks and Jones (1958) test

Parameter	Days to maturity	Seed yield	Biomass yield	Harvest index	1000 seed weight
M	2.151±0.007*	3.305±0.078*	3.666±0.081*	1.647±0.013*	0.757±0.015*
[d]	-0.027±0.001*	0.079±0.004*	0.064±0.008*	0.015±0.004*	-0.015±0.011^{ns}
[h]	-0.045±0.017*	-0.231±0.235^{ns}	-0.244±0.243^{ns}	0.014±0.041^{ns}	-0.300±0.040*

* - Significant (if the value of parameter divided by its standard error exceeds 1.96)

the alleles responsible for low value of traits were over dominant over the alleles controlling high value were contributed to dominance gene effects (Cukadar-Olmedo and Miller, 1997). These outcomes are similar with results of rice crop in tiller number, panicle number and 1000 grain weight (Kiani et al., 2013).

The remaining traits namely number of finger and seed yield at Adet whereas finger length at Mecha had shown predominance of additive effects than dominance component, this may indicating selection of characters are effective in early generations (Khattab et al., 2010). These results are similar with previous researcher (Hailu and Peat, 1997) on tef and (Marimuthu and rajagopalan, 1997) on finger millet, whereas contrary to the above idea, (Kiani et al., 2013) report on the inheritance of panicle length. The estimates of additive gene effects (d) were also found negative. The negative or positive sign for additive effects depends on which parent is chosen as P1 (Mather and Jinks, 1982; Cukadar-Olmedo and Miller, 1997).

Among the existence of epistasis gene action additive × additive effect is important for plant breeders and genetic improvement of traits via selection. It was significant for finger length, number of tiller, number of finger, days to maturity and thousand seed weight at both locations whereas harvest index alone found at Mecha. Selection method can be used to fix the genes, but when negative sign occurred like above revealed traits, selection should be delayed to later generations. Thus to obtained the advantage, recurrent selection method could be chosen for the improvement of these traits (Singh and Narayanan, 2000). This result are also in close agreement for days to maturity, seed yield, 100 kernel weight and number of spikes/plant of wheat with various reports (Hendawy, 2003; Moussa, 2010; Mohamed and Khaled, 2013). Except days to maturity at locations and number of tiller at Mecha, the other studied traits described dominance x additive type of epistasis was non-significant; which implied that inheritance of the traits in the cross are not found for such type of epistasis.

The greater magnitude of non-allelic interaction had shown dominance x dominance type of interaction in the present study. It was found positive for all significant traits such as: finger length, number of finger, seed yield, harvest index and thousand seed weight at both locations; and days to maturity at Adet. The dominance x dominance interaction higher magnitude over other epistasis type of gene effects as well as its positive findings in the genetic inheritance system verify the imperative function of it in controlling these traits for two locations. These findings are in congruence with those results achieved on wheat (Hendawy et al., 2009; Mohamed and Khaled, 2013). The study of different types of gene effects revealed that epistatic gene effects were as important as additive and dominance gene effects for most of the traits and it can allow generating different phenotypes, some of which represent real genetic advance over their parents (Allard, 1960). This revealed that selection favored at later generations for enhancement of genetic gain to improvement of finger millet seed yield.

The gene effect that express the direction of the population mean depends on the signs associated with estimates of types of epistasis namely additive x additive [i], additive x dominance [j] and dominance x dominance [l]. As, Mather and Jinks (1982) reported that the information on the association or dispersion of genes in the parents could be found based on, the sign of [i], [j] and [l] on studied traits. Accordingly, among the types of epistasis, complementary type identified in most traits such as: seed yield and harvest index in both locations and similarly number of finger at Adet and finger length, number of tiller and number of ear at Mecha. This implied that the dominance and dominance x dominance type of gene effect shown the same sign and associated in both studied areas; as a result the traits are easily exploitable (Singh and Pawar, 2005). Hence, in this study will produce new recombinants that have possibility of improving of genetic gain and yield in breeding programme (Alake et al., 2012).

Duplicate type of epistasis was seen on days to maturity and thousand seed weight at both location and additionally finger length and number of tiller at Adet and number of finger at Mecha, since Dominance and dominance x dominance parameters displayed opposite signs. Those traits mentioned above are controlled by duplicate epistasis have influence on variability in segregating generations and become difficult to exploit them, since it hinder the selection process (Kumar and Patra, 2010). The opposite signs of dominance and dominance x dominance gene effect have an equal and opposing effect each other, hence it is difficult to utilize and leading to reduced heterosis in breeding work (Shashikumar et al., 2010) which is due to the presence of predominantly dispersed alleles at the interacting loci in a duplicate-type epistasis gene effect (Jinks and Jones, 1958). Thus, recurrent selection breeding method applied in exploiting any character depends on the gene action involved in its expression for late generation selection process to develop improved varieties.

CONCLUSION

The variance analysis revealed that all generations had adequate genotypic variation to make genetic analysis for all traits. This study found absence of maternal effects for any of the investigated traits, which indicated the possibility of using any high yielding parent as female parent in finger millet crossing program in the future. The individual scaling test was non-significant for traits such as plant height and days to flowering in both locations; whereas, number of ear and biomass yield additionally found at Adet. On the contrary, other traits have been influenced at least with one non-allelic interaction. Significant additive and dominance gene main effects were observed for number of tiller and days to maturity in both locations and also seen additionally on number of finger and number of ear at Mecha. Additive gene effects showed preponderance on number of finger and seed yield at Adet whereas finger length at Mecha. In connection to this additive x additive gene effect showed significant difference in most studied traits. The presence of negative sign also indicates improvement of the traits is achieved at later generations. Likewise, complementary type of epistasis were found in most traits particularly in seed yield and harvest index in both locations than duplicate type of epistasis, implying that the crop improvement for traits controlled by this type of epistasis is easily exploitable. Based on the results it could be depicted that yield and its contributing traits exhibited all three types of gene actions, i.e. additive, dominant and epistasis. In such situation, selection and recombination breeding could be used to later generations. Therefore, improvement in studied finger millet traits to develop improved varieties will require a recurrent selection method; that may exploit first additive gene effects and succeeding to non-additive gene effects through standard selection procedures.

AUTHOR CONTRIBUTIONS

All the authors contributing their comments from proposal set up to final manuscript write up. However, Wossen Tarekegne did the experiment, collects data and analyses it.

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COMPETING INTERESTS

The authors declare that they have no conflicts of interest associated with the publication of this article.

ETHICS APPROVAL

Not applicable

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