Heritability, Genetic Advance and Gene Action Determination for Seed Yield and Yield Components Using Generations of Finger Millet [*Eleusine coracana* (L.) Gaertn]

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Abstract: *Finger millet (Eleusine coracana (L.)Gaertn.) is a small seed crop grown in low rainfall areas and its diverse cultural conditions make it an important food security crop; however, its productivity is low in Ethiopia. This research was done to estimate heritability and gene numbers for yield and yield components in parental, filial and backcross generations derived from a cross of two-finger millet cultivars at Koga and Adet Agricultural Research Centers, Northwestern Ethiopia in 2014/15. The experiment comprised six basic generations and four reciprocals of finger millet evaluated in randomized complete block design with two replications. Data on yield and yield component traits were recorded. The result showed the number of genes estimated in both locations ranged from -0.23 to 88.78, indicating that the presence of many genes with small cumulative effect and epistasis gene effect will bias an estimate of the number of genes. Medium to high narrow-sense heritability value coupled with high genetic advance showed the influence of additive variance and ease of improvement for biomass yield and number of ears in this population. While low, medium and high narrow-sense heritability observed together with the low genetic gain in most traits; which showed the presence of small additive variance in most traits with the influence of epistasis; hence intensive selection is required to exploit the characters. In most traits, the number of genes estimated to be negative and/or very small indicates that epistasis was significant and the existence of environmental effect in both locations. The results indicate the presence of genetic variability for developing improved varieties through crossing and selection.*

Keywords: Additive variance, Epistasis, Genetic variability, Polygene

1. Introduction

Finger millet [*Eleusine coracana* (L.) Gaertn] is an important staple crop grown under rain-fed conditions in Northwestern Ethiopia which has 96.9% area coverage from the Amhara region (CSA, 2020). The total area coverage of finger millet in Ethiopia is 455,580.47 ha with a total production of 112595.79 tons whereas in Amhara Region it covers 236,124.66 ha of land with the production of 59140.23 tons, which has a proportion of 51.83% and 52.5% to the national area coverage and production, respectively (CSA, 2020). However, it is the most neglected cereal crop grown on marginal lands under poor management condition and resulted in very low yield (Salasya *et al*., 2009). Degu *et al*. (2009) 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 overall progress of the crop in developing countries; even though environmental factors also contribute to large losses in yield (Zerihun, 2009).

The knowledge of genetic system present in a given crop species of the character under improvement is of paramount importance for the success of any plant-breeding program (Azizi *et al*., 2006). Hence, estimation of genetic parameters helps researchers understanding genetic variances, heritability, and the number of genes and to facilitate the selection of a desirable breeding method.

The basic and key to bringing about genetic improvement in any crop is the availability of genetic variability. Variability is the occurrence of differences among individuals due to differences in their genetic composition and/or the environment in which they are raised (Allard, 1960; Falconer *et al*., 1996).

Heritability of crops provides information used for breeders in designing appropriate breeding strategies. The magnitude of such estimates also suggests the extent to which improvement is possible through selection. However, Johnson *et al.* (1955) stated that heritability estimates together with genetic advance are more important than heritability alone to predict the resulting effect of selecting the best individuals. Likewise, Bisne *et al*. (2009) also reported that heritability estimates along with genetic advance are normally more helpful in predicting the gain under selection than heritability estimates alone. Genetic advance is also of considerable importance because it indicates the magnitude of the expected genetic gain from one cycle of selection (Hamdi *et al.*, 2003). Genetic advance as percent of the mean (GAM) is a more reliable index for understanding the effectiveness of selection in improving the traits because the estimates are derived by the involvement of heritability, phenotypic standard deviation and intensity of selection. Thus, genetic advance (GA) along with heritability provides a clear picture regarding the effectiveness of selection for improving the plant characters.

In order to develop a high yielding variety, it is very important to know about the genetic structure of each trait including, variability, gene mode of action, heritability and number of controller genes. This information enables breeders to develop improved varieties. Hence, the present investigation is carried out to gather information on heritability and the number of genes governing the expression of yield and yield component traits of finger millet to design appropriate breeding strategies

2. Materials and Methods

2.1. Description of the study area

The study was undertaken in the Northwestern Ethiopia at the research field of Mecha and Adet Agricultural Research Center.

Table 1: Geographical description of the experimental sites

Location	Elevation (masl)	Latitude	Longitude	Temperature (°C)		Annual rainfall (mm)
				Maximum	Minimum	
Mecha	1960	11°25’20” N	37°10’20” E	27.9	9.4	1557.9
Adet	2240	11°16’19’’N	37°28’38’’E	26.4	10.9	1215.2

Source: WAMSC, 2014

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*; NSRC, 2006**; O.M = Organic matter; ppm = parts per million

2.2. Experimental materials

The experimental materials produced using generation mean analysis, with model parameters of (m), (a) and (d) that consisted of basic generations (P1, P2, F1, F2, BC1, and BC2) and their reciprocals (RF1, RF2, RBC1 and RBC2) derived from a cross of improved variety Necho (P1) and local Tikur dagusa/Abate tikur (P2). The parent varieties were chosen primarily based on their difference in seed yield, yield components and other traits.

2.3. Experimental design

The six basic generations and their four reciprocals were evaluated in a Randomized Complete Block Design with 2 replications at the research field of Mecha and Adet Agricultural Research Center. Each plot for various generations was sown in one, two, and three rows with five-meter lengths for parental, F1 and RF1 generations; for backcross and reciprocal backcross and for F2 and RF2 generations, in the same order (Akhtar and Chowdhary, 2006; Yadav and Singh, 2011). Each generation was planted in a plot of 5 m length with row to row spacing of 40 cm and a within row spacing of 15 cm.

2.4. Management of experimental plants

The seed rate of 15 kg/ha and fertilizer rate of 100/50 kg/ha for DAP and UREA were applied in rows, respectively (Molla, 2012). The total required amount of phosphorous applied at basal but from the total nitrogen applied half was used at planting and the remaining was top-dressed at tillering stage. Hand hoeing and weeding were made one and two times, respectively over the growing season to put the experimental plots free of weeds. Other agronomic management practices were done as required.

2.5. Data collection

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, sampled numbers were 10 plants for non-segregating generations such as P1, P2, F1 and RF1 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).

The measured traits on a plant basis included plant height, number of effective tillers, number of ears, number of fingers/ear and finger length data were recorded. Other parameters such as days to flowering, days to maturity, grain yield, biomass yield, harvest index and thousand seed weight were recorded on a plot basis. The measurement was done according to the International Board for Plant Genetic Resources (IBPGR, 1985) descriptor.

2.6. Data analysis

Analysis of variance and mean comparison using Duncan’s Multiple Range Test at 5% probability level was done with SAS statistical software model with computer application (SAS, 2002).

2.6.1. *Generation variance component analysis*

Variance components under generation mean analysis (additive, dominance and environment) were estimated as per Kearsey and Pooni (1996) and Mather and Jinks (1971) using the following equations.

$$V(E) = \frac{1}{4}(VP1 + VP2 + 2VF1 \qquad [1]$$

Where:

V(E) = Environment variance; VP1 = Variance parent one; VP2 = Variance parent two and VF1 = Variance first filial generation

$$V(A) = 2VF2 - VBC1 - VBC2 \qquad [2]$$

Where:

V(A) = Additive variance; VF2 = variance second filial generation; VBC1 = Variance backcross one and VBC2 = Variance backcross two

$$V(D) = 4(VF2 - \frac{1}{2V[d]} - V[E]) \qquad [3]$$

Where:

V(D) = Dominance variance; VF2 = Variance second filial generation; V[d] = Variance dominance and V[E] = Environmental variance

$$\left(\frac{D}{A}\right)1/2 = \left(\frac{V[D]}{V[A]}\right)1/2 \qquad [4]$$

Where

$\left(\frac{D}{A}\right)1/2$ = Average degree of dominance variance; V[D] = Dominance variance; V[A] = Additive variance

$$F = VBC1 - VBC2 \qquad [5]$$

Where

F = Association between D and A in all loci; VBC1= variance backcross one; VBC2 = variance backcross two

2.6.2. *Heritability analysis*

Narrow sense heritability (h^2n) was estimated following the methods described by Warner (1952).

$$h2n = [2VF2 - (VBC1 + VBC2)]/VF2 \qquad [6]$$

Where:

h^2n = narrow sense heritability; VBC1 variance backcross one; variance backcross two; variance second filial generation

According to Robinson *et al*. (1949) heritability (H^2) with the values of $H^2<0.2$ is classified as low while, values between 0.2 and 0.4 and greater than 0.4 are considered as moderate and high, respectively.

2.6.3. *Genetic advance analysis*

Genetic advance i.e. the expected genetic gains from selection were calculated using the formula described by Johnson *et al*. (1955) indicated under formula 7 while the predicted genetic advance where the expected genetic gain upon selection was expressed as a percentage of F2 mean using the formula under 8.

$$\Delta G = K * h2n * \sigma F2 \qquad [7]$$

Where:
ΔG = Genetic advance; h^2n = narrow sense heritability; $\sigma F2$ = standard deviation second filial generation

$$\Delta G(\%) = \left(\Delta G * \sqrt{F2}\right) * 100 \qquad [8]$$

Where:
ΔG (%) = Genetic advance as percentage of second filial generation; F2 = second filial generation

2.6.4. *Minimum number of gene analysis*

In order to evaluate the effect of those genes which are involved in yield and yield component traits minimum number of gene was computed using the formula described by Lande (1981).

$$MNG = \frac{(\overline{P1} - \overline{P2})^2}{8[2\sigma^2 F2 - (\sigma^2 BC1 + \sigma^2 BC2)]} \qquad [9]$$

Where:
MNG = Minimum number of gene; P1 =parent one cultivar; P2 = Parent two cultivar; σ^2 = variance; F2 = second filial generation; BC1 = Backcross one; BC2 = Backcross two

3. Results and Discussion

3.1. Analysis of variance

Analysis of variance indicated the presence of significant differences ($P \leq 0.01$) among generation for all traits at Adet (Table 3) and for all traits except plant height ($P \leq 0.05$) at Mecha (Table 4). A significant difference between treatments indicated the existence of genetic variability in genetic materials for the traits studied. These results were in agreement with the findings of Foroozanfar and Zeynali (2013) in bread wheat. The foregoing statement ensures the presence of high genetic potential among these generations so that these results are similar as generation effects found significantly different as suggested by Dvojković *et al.* (2010).

Table 3: Analysis of variance of yield and yield component 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 component traits of all 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 Weight

3.2. Mean performance of the generations

The mean performance of the generations for yield and its components are presented in Table 5and Table 6. The results revealed the presence of genetic variability for these characters in the studied materials. The F1's mean value for all traits except plant height, days to flowering, days to maturity and thousand seed weight were greater than the mid parental value of finger length, number of tillers, number of fingers, number of ears, seed yield, biomass yield and harvest index.

The F2's mean value was significantly below that of the F1's, except for traits days to flowering, days to maturity and thousand seed weight; whereas, its mean value was better than the mid-value of parental lines for the traits finger length, the number of fingers, days to maturity, seed yield, harvest index and thousand seed weight. The backcross to P1 was significantly different from backcross to P2 excluding thousand seed weight character at Adet (Table 5). Similarly, at Mecha the F1's mean value was greater than to the mid parent and mean of F2's value of all traits except to days to flowering, days to maturity and thousand seed weight. Backcross to P1 was significantly different from backcross to P2 except for seed yield, harvest index and thousand seed weight (Table 6).

Table 5.The mean, standard error and DMRT 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±1.0^{d}	130.50±0.5^{e}	2387.35±57.10^{b}	4966.00±484.0^{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±0.5^{a}	149.00±1.0^{a}	1550.68±76.68^{e}	4305.00±395.0^{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±1.5^{bc}	135.00±0.0^{c}	3203.85±109.55^{a}	5188.50±418.5^{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±1.5^{bc}	140.50±0.5^{b}	2139.30±57.00^{c}	4592.50±307.5^{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±2.0^{c}	133.00±0.0^{d}	2233.83±50.63^{c}	4622.50±519.5^{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±1.0^{b}	139.50±0.5^{b}	1844.35±131.75^{d}	4301.50±299.5^{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±0.5^{bc}	135.50±0.5^{c}	3178.30±124.30^{a}	5220.00±294.0^{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±1.5^{bc}	140.00±1.0^{b}	2127.40±107.10^{c}	4632.50±354.5^{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±2.0^{c}	133.00±0.0^{d}	2210.25±101.25^{c}	4631.50±401.5^{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±1.0^{b}	139.50±0.5^{b}	1849.45±148.95^{d}	4288.00±288.0^{c}	43.09±0.59^{cd}	3.00±0.00^{b}

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 DMRT 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±0.5^{d}	121.50±0.5^{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±0.0^{a}	137.50±0.5^{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±0.0^{c}	129.00±1.0^{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±1.0^{c}	134.00±1.0^{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±0.5^{c}	129.50±0.5^{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±0.0^{b}	133.00±0.0^{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±0.0^{c}	129.50±0.5^{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±1.0^{c}	134.50±0.5^{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±1.0^{c}	129.50±0.5^{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±1.0^{b}	133.00±0.0^{b}	1752.50±102.50^{c}	3675.50±258.50^{c}	47.73±0.58^{bc}	3.05±0.05^{cd}

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

3.3. Component of genetic variation

Mather (1943, 1973) stated that genetic variability obtained because of crossing, segregation and recombination of parental lines redistributed among the various states, in which it can exist. The existence of genetic variation in the cross shows how much of the variation is heritable and what types of gene effects are involved. Estimates of additive, dominance and environmental variances, degree of dominance, the direction of dominance, heritability values, genetic advance and number of genes are presented in Table 7 and Table 8.

Table 7: Variance components estimates of generations for various characters of finger millet 'Necho x Tikurdagusa' cross at Adet

Traits	A	D	E	$(H/D)^{1/2}$	F	MNG
Plant height (cm)	-0.000045	0.000355	0.000031	-2.81	0.000157	-10.63
Finger length (cm)	-0.001142	0.00166	0.000243	-1.21	-0.000884	-1.29
Number of tiller	-0.001749	0.003864	0.000121	-1.49	-0.000093	-0.27
Number of finger	-0.000249	-0.00262	0.000789	3.24	0.000035	-7.76
Number of ear	0.007348	0.002888	0.012312	0.63	0.003896	2.44
Days to flowering	-0.000013	0.000332	0.000041	-5.05	0.000153	-6.9
Days to maturity	0.000033	-0.000022	0.000008	-0.82	-0.000005	12.37
Seed yield	-0.001411	0.003016	0.000593	-1.46	-0.001531	-3.12
Biomass yield	-0.002061	0.001018	0.002512	-0.7	0.001847	-0.23
Harvest index	-0.000503	-0.000624	0.000654	1.11	0.000977	-2.42
1000 seed weight	-0.000151	-0.000068	0.000142	0.67	0.000249	-0.36

A = Additive variance, D = Dominance variance, E = Environmental variance (E), $(D/A)^{1/2}$ = Degree of dominance, the F = Direction of dominance, MNG = The minimum number of gene

Table 8: Variance components estimates of generations for various characters of finger millet 'Necho x Tikurdagusa' cross at Mecha

Traits	**A**	**D**	**E**	$\mathbf{(H/D)^{1/2}}$	**F**	**MNG**
Plant height (cm)	0.000093	-0.002254	0.000587	-4.92	-0.000033	5.96
Finger length (cm)	-0.000112	-0.000164	0.000165	1.21	0.000004	-10.94
Number of tiller	0.000393	0.000564	0.000516	1.20	0.001207	5.38
Number of finger	-0.000484	-0.002399	0.000853	2.23	-0.00006	-8.1
Number of ear	-0.000306	-0.001312	0.000624	2.07	-0.00029	-8.82
Days to flowering	0.00003	0.000072	0.000009	1.55	0.000034	4.99
Days to maturity	0.000004	-0.000008	0.000005	-1.41	0.000006	88.78
Seed yield	-0.003037	0.005776	0.000081	-1.38	0.000933	-1.03
Biomass yield	-0.003221	0.00346	0.000746	-1.04	0.000051	-0.64
Harvest index	-0.000064	-0.001232	0.000342	4.39	-0.00003	-1.68
1000 seed weight	0.000007	-0.00107	0.000272	-12.36	-0.000009	16.45

A = Additive variance, D = Dominance variance, E = Environmental variance (E), $(D/A)^{1/2}$ = Degree of dominance, the F = Direction of dominance, MNG = The minimum number of gene

3.3.1. *Additive variance*

The predominance of additive gene action depicted that it is fixable in nature and selection will be very effective, but the existence of low and negative additive variance in most traits in this cross-required intensive selection to exploit the traits due to the presence of epistasis gene effect. The negative value of dominance and additive variances for the characters indicates that the negative sign may arise due to genotype by environment interaction (Robinson *et al.*, 1955; Haque *et al*., 2013). The environmental variance was higher than the additive variance for the number of fingers, number of ears, and harvest index at both locations and days to flowering and biomass yield at Adet. Whereas, plant height, finger length, number of tillers, days to maturity and thousand seed weight at Mecha, which indicated that, this character lacks value for selection in this cross. At the same time, estimates of low narrow-sense heritability for these traits were also other indicators for a low value of additive variances. This suggests that the environment and non-additive gene effect had influenced the expression of the yield and yield component traits. Therefore, breeding methodologies that can reduce these variations may help improve the rate of gain from the traits; and suggesting that additive variance was playing a major role in the improvement of these traits.

3.3.2. *Average degree of dominance*

The average degree of dominance revealed high variation in both sites. It ranged from 0.63 (number of ears) to -5.05 (days to flowering) at Adet and -1.04 (biomass yield) to -12.36 (thousand seed weight) at Mecha site (Table 7and Table 8). According to Kearsey and Pooni (1996) and Farshadfar (1998) average degree of dominance is used to determine the importance of dominance effects in relation to the additive deviations of genes and is estimated as partial when the value was less than unity while dominance was greater than unity for traits influenced by over-dominance effects. Hence, in this study partial dominance, dominance and over dominance gene effects present in the inheritance of traits with the range of 0.63 to -12.36.

The results indicated that except the number of ears/plant, days to maturity, biomass yield and thousand seed weight at Adet and biomass yield at Mecha; the other traits in both locations determined by over dominance gene effects. Kutlu and Olgun (2015) reported similar findings where over dominance gene effect was observed for harvest index and grain yield per plant in the mean of average degree of dominance value. This foregoing statement showed a low, narrow-sense heritability because of a strong environmental effect on the expression of this trait.

3.3.3. *Direction of dominance*

The direction of dominance (F) estimated for the studied traits (Table 7and Table 8)showed positive value for most of the traits except for finger length, number of tillers/plant, days to maturity and seed yield at Adet, and plant height, number of fingers, number of ears, harvest index and thousand seed weight at Mecha. These results indicated that the traits controlled by dominant gene action so that dominant alleles were found more than recessive alleles in the parents. Likewise, Shahrokhi *et al*. (2013) observed the importance of dominant gene action in the inheritance of the above traits. The negative values of F mean, the additive genetic variation controlled the inheritance of the traits. Selection methods are effective to improve these traits in this cross.

3.3.4. *Minimum number of genes*

Determination of the number and effects of this polygene desired for obtaining optimal genotypes in breeding practice. Hence, estimates of the minimum number of genes controlling yield and yield-related traits are shown in Table 7and Table 8. The estimates of both locations ranged from -0.23 to 88.78 number of genes.

According to individual location estimated number of genes ranged from -0.23 (biomass yield) to 12.37 (days to maturity) at Adet whereas from -0.64 (biomass yield) to 88.78 (days to maturity) at Mecha were controlled by many genes and this happened because of divergence of the two parents, so these cultivars can be used for future breeding programs as genetic materials. The negative sign and small values of the number of genes may indicate the presence of epistasis and environmental effect (Coates and White, 1998). Similarly, Yield and its component traits controlled by polygene, whose expression greatly affected by environments (Ahmed and Khaliq, 2007). Therefore, the estimates of the minimum number of genes of the cross are likely to be inaccurate with the effect of environment and epistasis. Despite a situation, most of the estimates indicate that the yield and its components are quantitatively inherited traits that are amenable to selection.

3.4. Heritability

Heritability estimates for studied characters between Adet and Mecha varied considerably and presented in Table 9, respectively. Narrow-sense heritability estimated in the range of 3.4 (days to flowering) to52.4 (days to maturity) at Adet and 0.52 (thousand seed weight) to 43.37 (biomass yield) at Mecha, respectively. The high heritability of days to maturity and thousand seed weight at Adet and biomass yield at Mecha estimate indicates the selection procedures are simpler and lead to fast genetic improvement of the traits (Khan et *al*., 2008) since these traits are highly heritable from parents to progenies. In addition to that, for traits that expressed high to medium heritability, simple selection would be an effective method (Feyissa and Zinaw, 2014). While, low heritability values were indicating selections might be difficult or virtually impractical and revealed only slow progress for the characters due to some variances constituting the environment variance or the masking effect of environment on genotypic effects (Eid, 2009). The estimated values of narrow-sense heritability (h^2n) were higher in some of the traits in both studied areas due to additive variance being higher. These indicated that additive gene action engaged in the expression of these traits and then selection becomes effective from segregate generations to obtain high performing cultivar (Kutlu and Olgun, 2015).In contrary to the above finding, the additive variance was lower than the environmental variance for traits found in Adet (days to flowering and biomass yield), Mecha (plant height, finger length, number of tillers, days to maturity and thousand seed weight) and in both locations (number of fingers/plant, number of ears/plant and harvest index). This may be suggesting the influence of environmental factors in the inheritance of these characters.

The traits such as plant height, number of finger and days to flowering at Adet and plant height, number of fingers, number of ears and harvest index at Mecha detected low narrow-sense heritability; this condition may happen when dominance and epistasis gene effects are increased (Warner, 1952). This is because of narrow-sense heritability depending on additive variance only.

Therefore, traits with low to high narrow-sense heritability indicated the occurrence of complex inheritance for the traits studied. Hence, the recurrent selection method required for the improvement of traits since it allows recombination and breaking up of undesirable linkage (Ganesh and Sakila, 1999). This cyclic method should continue until a high level of gene fixation attained with early and intensifies selection of later generations (Arora *et al*., 2010).

3.5. Genetic advance

The estimated values of genetic advance and genetic advance as percent of F2 mean for different characters are presented in Table 9. Selection efficiency depends on both heritability and genetic advance as indicated by Johnson *et al*. (1955) and Ubi *et al*. (2001) because the genetic advance is a useful indicator when selection applies to the relevant population to predict the progress that can be expected. In the present study, high heritability coupled with high genetic advance noticed for biomass yield at Mecha while medium heritability along with high genetic advance was recorded for the number of ears and biomass yield at Adet. This indicated the additive nature of genetic variation transmitted from the parents to the progeny. In addition, this trait can easily fix in the genotypes by selection in early generations. These results were in harmony with the finding of the previous researcher (Yadav *et al*., 2011) for biological yield. The information on heritability and genetic advance ascribed the additive gene effects are may be more essential for the above traits than non-additive effects and can be improved through simple or progeny selection methods (Johnson *et al*., 1955; Panse, 1957).

Medium to high heritability accompanied by low genetic advance for finger length, number of tillers, seed yield, harvest index, days to maturity and thousand seed weight at Adet; similarly, finger length, number of tillers, days to flowering, and days to maturity, seed yield and thousand seed weight at Mecha. The result showed that the traits could be improved by inter-mating superior genotypes of segregating population developed from a combination of genotypes with recurrent selection method since non-additive gene actions' was predominance than other gene action. In agreement with this study, consistent estimates reported in previous studies of Yadav *et al*. (2011).

Low heritability with low genetic advance values found for plant height and number of finger and days to flowering at Adet while plant height, number of finger, number of ear and harvest index at Mecha, indicating slow progress through selection for these traits. The reason for the low heritability for these characters was a result of some variances constituting the environment variance. These results find support from the earlier study reported (Eid, 2009) for plant height and number of grain.

Table 9: Estimates of heritability, genetic advance, and genetic advance at a percentage of mean at Adet and Mecha

Traits	Adet			Mecha		
	h^2n	ΔG	ΔG (%)	h^2n	ΔG	ΔG (%)
Plant height	10.4	0.0021	0.29	3.17	0.0005	0.07
Finger length	37.5	0.0067	0.69	25.4	0.003558	0.37
Number of tiller	30.5	0.01332	1.34	26.7	0.046917	4.19
Number of finger	6.8	0.00013	0.01	13	0.000295	0.03
Number of ear	32.6	1.12204	117.95	13.6	0.004006	0.4
Days to flowering	3.4	0.0008	0.11	27.03	0.002339	0.33
Days to maturity	52.4	0.0021	0.31	23.53	0.000242	0.04
Seed yield	28.1	0.037	6.75	34.15	0.000422	0.08
Biomass yield	36.9	0.132	25.26	43.37	89.34	16963.31
Harvest index	28.2	0.0143	1.85	3.91	0.000016	0.002
1000 seed weight	41.8	0.00423	0.34	0.52	0.000009	0.0007

4. Conclusion and Recommendations

According to generation variance analysis additive, genetic variance and dominance genetic variance influenced the expression of finger millet traits. This indicated that both additive and non-additive gene action involved in the control of traits. The average degree of dominance values indicated that number of ears, biomass yield and thousand seed weight at Adet showed partial dominance, while the other traits implied over dominance gene actions. Medium to high narrow-sense heritability value coupled with high genetic advance showed the influence of additive variance and ease of improvement of these important traits in this population. While low narrow-sense heritability along with low genetic advance indicated the occurrence of complex inheritance for the traits studied. Hence, the recurrent selection method required for the improvement of traits since it allows recombination and breaking up of undesirable linkage. The number of genes governing the inheritance of the characters in both locations ranged low to high indicating the inheritance of the traits depends on polygenic action. In connection to this, the result showed the presence of dominance and epistasis, which bias an estimate of a minimum number of genes. Besides, the small and negative value of the number of genes on the study traits indicated the probable presence of epistasis and environmental effects. The results of this study concluded the existence of sufficient genetic variability as well as additive and non-additive type of gene effects in the inheritance of the traits. Therefore, the possibility of developing lines and hybrids were showed clearly in this study; so that, improvement of high heritability coupled with high genetic advance noticed for biomass yield at Mecha while medium heritability along with high genetic advance was recorded for the number of ear and biomass yield at Adet. Medium to high heritability accompanied by low genetic advance for finger length, number of tillers, seed yield, harvest index, days to maturity and thousand seed weight at Adet; similarly, finger length, number of tillers, days to flowering, and days to maturity, seed yield and thousand seed weight at Mecha. These indicated the presence of additive, dominance and epistasis gene action and its improvement could be achieved through recurrent selection at early and later generations.

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