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# Genetic analysis of earliness in Scarlet (*Solanum aethiopicum* L.) Gboma *(Solanum macrocarpon* L.) and *Solanum anguivi*

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## ABSTRACT

Late commencement of rainfall, delayed flowering and variation in growth cycle necessitate development of early and medium maturing varieties of crops. In this research, we evaluated inheritance pattern, genetic control, heritability and heterosis of earliness in intraspecies and interspecies hybridization in Scarlet, Gboma and *S. anguivi*. Interspecies and intraspecies crosses were made to develop five and six generations. Parents and segregating population were planted in compact family block design with three replications. Earliness was estimated as the number of days from transplanting to 50% flowering. The findings showed overwhelming evidence of interaction among multiple genes for earliness. Additive gene effect contributed significantly to earliness in the cross $Ab_2$ × Var 19 and Fovembot-2 ♂ × $Db_3$ ♀. Dominance effects were more important and favoured late flowering. Additive effects governed inheritance of earliness compared to dominance gene in intraspecies cross Var 26 ♂ × Var 24 ♀ (*S. aethiopicum*) and MM 268 ♂ × MM 150 ♀ (*S. macrocarpon*). Duplicate epistasis in the cross $Ab_2$ ♂ × Var 19 ♀ hindered development of early flowering varieties through selection, and decreased variation in $F_2$ and subsequent generations. Preponderance of additive gene effect coupled with high narrow sense heritability for earliness indicates that development of early flowering and maturity varieties will be achieved. Inheritance of earliness is polygenic with stable performance. Considerable heterosis for earliness was associated with the superiority of the $F_1$ over the mid parent, and sufficient divergence among the parents.

**Keywords:** African eggplant, additive effects, dominance gene, duplicate gene action, recurrent selection, hybridization

## INTRODUCTION

African eggplants (*Solanum aethiopicum* L., *Solanum anguivi* L., *Solanum macrocarpon* L.) are classified in the genus Solanum, subgenus *Leptostemonum* (Dunal). Both *Solanum melongena* and *S. macrocarpon* are in the section *Melongena*. The wild ancestor of all the cultivar groups in *S. aethiopicum* is *Solanum anguivi* (Bukenya, 2004). Scarlet eggplant (*S. aethiopicum*) is an important vegetable (fruits and leaves) in tropical Africa, especially in the less humid regions. In *S. aethiopicum,* four cultivar-groups are recognized: Gilo, Kumba, Shum and Aculeatum (Daunay *et al*. 2001; Lester and Hawkes, 2001; Lester and Daunay, 2003). Eggplant is self-pollinated, flowers are bisexual and out crossing ranges between 30 and 45%, inflorescences are with short cymes or

trusses (Shippers, 2002; Bukenya and Bonsu, 2004). Solitary flowers and cymes are mostly found in the Kumba group, whereas trusses are common in the Gilo and Aculeatum, this is linked to fruit number and size (Bukenya, 2004). Stigma receptivity had been observed to start on the day before anthesis, whereas pollen viability occurs on the day of anthesis or a day later and can remain so for up to 2 days later, and abortion of floral structures in Solanum species is associated with physiological, genetic and environmental factors (Bukenya and Carasco, 1994; Bukenya, 2004).

Hybridization among *S. aethiopicum*, *S. anguivi* and *S. macrocarpon* using large flower (*S. macrocarpon*) as pollen parent and the smaller flower (*S. aethiopicum and S. anguivi*) as maternal parent recorded high success rate (Shippers, 2002). Physiological incompatibility, poor pollen germination and seedless fruits were encountered when the order was reversed. *Solanum aethiopicum* and *S. anguivi* are easily crossed and progenies developed are highly fertile (Omidiji, 1979). Attempts at crossing eggplant with its wild relatives resulted in limited success due to sexual incompatibility associated with variation in ploidy level and complex floral biology.

Days to first flowering are an indicator for earliness. It takes on the average 65 days (d) (between 58 d and 72 d) for *Solanum aethiopicum* to flower, after four weeks in the nursery. *Solanum macrocarpon* flowers 76 d (between 64 d and 88 d), and *S. anguivi* flowers 92 d (between 74 d – 98 d) (Adeniji *et al.,* 2012; Adeniji, 2013). Preference for early, medium and late maturing varieties among eggplant growers lends weight to the importance of developing early or medium maturing varieties (Adeniji and Aloyce, 2012). Earliness is highly desirable attribute in African eggplants, as the market prices are invariably high during early harvest in the season and off season. Eggplant fruits harvested early in the season are firm, fresh, crispy, succulent and tasty with moisture, high total soluble solids and low cracking (Adeniji, 2012) and adequate biochemical characteristics (Collonnier *et al*. 2001 and Kashyap *et al*. 2003). On the other hand, fruits harvested from late maturing varieties lack freshness, poor taste, dry and fibrous with low total soluble solids (Adeniji, 2012). Development of early maturing varieties of African eggplants has not been the major focus of research in sub-Sahara Africa. Consequently, information on mode of inheritance and genetic control of earliness in African eggplants is limited. Transmissions of genetic information from one generation to another as well as the magnitude of heterosis are important in developing extra early, early and medium maturing varieties. The information will help to identify the appropriate selection methods for advancing promising segregating population with earliness gene. The objectives of this study were to evaluate the mode of inheritance and genetic action controlling earliness, estimate heritability and heterosis for earliness, and the effective factors for earliness in intra and inter species cross.

## MATERIALS AND METHODS

### Development of $F_1$, $F_2$ and Backcrosses Population

Seven accessions of African eggplant (Table 1) were selected considering their performance in previous for agronomic research. The $Ab_2$ and $Db_3$ were released varieties in Tanzania, Kenya and Uganda. They are moderate to high fruit yielding and medium maturing varieties.

**Table 1**. Source and attribute of parents used in development of hybrids of African eggplants.

| Genotypes | Species | Days to Flowering (days) | Source |
|---|---|---|---|
| Var 19 | *S. aethiopicum* | 82 | AVRDC |
| Var 24 | *S. aethiopicum* | 57 | AVRDC |
| Var 26 | *S. aethiopicum* | 80 | AVRDC |
| $Ab_2$ | *S. aethiopicum* | 56 | AVRDC |
| $Db_3$ | *S. aethiopicum* | 57 | AVRDC |
| MM 150 | *S. macrocarpon* | 63 | AVRDC |
| MM 268 | *S. macrocarpon* | 85 | AVRDC |
| Fovembot-7 | *S. anguivi* | 96 | AVRDC |

AVDRC = Asian Vegetable Research and Development Center

Seeds of each parent were raised in pots (12 cm by 23 cm) filled with sterilized soil and arranged in the screen house. Five pots were allotted to each accession. Due to variation in appearance of flower buds and flowering, nursery establishment and transplanting were staggered to synchronize flowering period. Pollination was carried out in the evening to take advantage of the cool weather and allow the pollen grains germinate through the style to fertilize the ovaries. Thereafter plants that were pollinated, identified and tagged. Hybridization was repeated after 13 hours to ensure success. Single crosses between Var 15 ♂ × $AB_2$ ♀, Var 26 ♂× Var 24♀ and MM 268 ♂× MM150♀ developed $F_1$ seeds, thereafter $F_1$ seeds were selfed to produce $F_2$ seeds. Backcrossing between $F_1$ and donor parent, $F_1$ and recipient parent produced seeds of backcross generation 1 and 2 ($BC_1$ and $BC_2$). Hybridization between $Db_3$ ♂ and Fovembot ♀ produced $F_1$ seeds, $F_1$ seeds were selfed to produce $F_2$ seeds, thereafter $F_3$ seeds. Backcross generations were not developed due to physiological incompatibility in the cross between Fovembot ♂ and $Db_3$ ♀.

**Population evaluation**

The five or six basic generations ($P_1$ and $P_2$), first, second and third filial generations ($F_1$, $F_2$ and $F_3$), first and second backcrosses generations ($BC_1$ and $BC_2$) from four cross combinations were evaluated for two years at the research field of Horticultural Training Research Institute, Arusha (latitude 4.88S, longitude 3.78E; altitude 1290m), Tanzania. The plots were 7 m long with a between-row spacing of 0.75 m and a within-row spacing of 35 cm. The field experiment was laid out in compact family block design with six blocks. Each of the blocks had three rows for each non-segregating generation ($P_1$, $P_2$ and $F_1$) and six rows for each segregating population ($F_2$, $F_3$, $BC_1$ and $BC_2$) and replicated three times. Seedlings were raised in multipot seedling trays and transplanted to the sides of the ridges at 0.45m between plants four weeks after sowing. At transplanting the plants were fertilized with NPK (20-10-10) at the rate of 90 kg N/ha, 45 kg $P_2O_5$/ha and 45 kg $K_2O$/ha. Urea was applied at the rate of 120 kg N/ha in three splits at one week after transplanting (WAT), at flowering and three weeks later. Ridomyl® (Matalxyl) WP (fungicide) was sprayed against damping off in the field at the rate of 20 g/15 litres of water 12 days after transplanting (DAT). Selecron EC (insecticide) was sprayed 2 (WAT) at the rate of 20 mls/20 litres of water to control cutworms and other insects. The experiment was furrow-irrigated every two days for the first 2 WAT; then once a week thereafter. Weeding was carried out manually and frequently with hoes to maintain weed-free plots.

**Data Collection and analysis**

Data were collected from 75 plants randomly picked from each parent, 200 plants from each $F_1$ generation and 300 plants for each $F_2$ generation while 275 plants were sampled for $F_3$ generation and 150 plants for each backcross generation. Homogeneity of variances of non-segregating generations was tested using Bartlett's test (Bartlett, 1937). Combined Analysis of variance was conducted to determine variation in earliness among generations. Separate analyses for each population were also performed for each year to determine within-plot variances using PROC ANOVA in SAS (2009). The individual scaling tests of Mather (1949) was performed for each year and across years to uncover possible involvement of non-allelic interaction among genes contributing to earliness. This tests uses data from $P_1$, $P_2$, $F_1$, $F_2$, $B_1$ and $B_2$ to provide estimates of the mean, additive and dominance effects. Those estimates are derived by the procedure of weighted least squares using as weights the inverse of the variances of generation means. The joint scaling test (Mather and Jinks, 1982) was also conducted. This test evaluates the goodness of -fit of the 3- parameter model (mean, additive and dominance effects) to the observed data by assuming that the sum of the squared deviations i.e (observed values – expected values)/2, weighted with appropriate coefficients follow a $X^2$ distribution with 3 df. Lack of fit implies the existence of non-additive gene effects other than dominance.

Generation mean was analyzed using the method of Hayman (1974) to fit a six parameter model. Those parameter, using Gamble's (1962) designation are the $F_2$ population mean or mean effect [m]; the pooled additive effect [a]; the pooled dominance effects, [d]; the pooled additive × additive epistatic effects, [aa]; the pooled additive by dominance epistatic effects, [ad]; and the pooled dominance × dominance epistatic effects, [dd]. $P_1$ will be the parents with higher mean value, $P_2$ the parent with a lower mean value, and $B_1$ and $B_2$ are corresponding backcrosses. The type of epistasis was determined only when dominance [d] and dominance × dominance [dd] effects were significant; when these effects had the same sign the effects were complementary, while different signs indicates duplicate epistasis (Kearsey and Pooni, 1996).

Narrow sense heritability ($H_2n$) estimates were computed as specified by Warner (1952) as $H_2n= [2F_2 – (VB_1 - VB_2)] /VF_2$ $(2F_2 – (VB_1, VB_2), VF_2$ denotes variance of the $F_2$ generation, $VB_1$ or $VB_2$ refer to the variance of the first and second backcross generations. Considering heterosis, the Absolute Mid-Parent Heterosis (AMPH) was computed as (AMPH) = F1 – MPV, Relative Mid-Parent Heterosis (RMPH) = [F1 – MPV/MPV] 100, Absolute High-Parent Heterosis (AHPH) = F1 – HPV, Absolute High Parent Heterosis (RHPH) = [$F_1$ – HPH/HPH] 100. The quantitative estimate of the minimum number of effective factors contributing to earliness was computed using Wright (1968) and Cockerham (1986).

**RESULTS**

The five ($P_1$, $P_2$, $F_1$, $F_2$, $F_3$) and six ($P_1$, $P_2$, $F_1$, $F_2$, $F_3$, $BC_1$ and $BC_2$) generations differed significantly ($P<0.01$) in days to flowering for each year and combined (Table 2). Since the analysis of variance showed significant ($P<0.05$) genotypic effects, generation mean analyses were conducted for each year and then two years were combined.

**Table 2**. Analysis of Variance for earliness in three cross combinations for two years in Arusha, Tanzania

| Source of Variation | Df | Var 15 × $AB_2$ | Var 26 × Var 24 | MM 268 ×MM150 | Fovembot × $Db_3$ |
|---|---|---|---|---|---|
| **Year 1** | | | | | |
| Replication | 2 | 15.05* | 11.56* | 4.38 | 2.40 |
| Generations | 5 | 483.28** | 275.15*** | 223.55** | (4)878.46** |
| Error | 10 | 5.92 | 5.02 | 5.92 | 1.31 |
| CV | | 3.75 | 3.45 | 6.43 | 1.62 |
| Mean | | 65 | 65 | 70 | 71 |
| **Year 2** | | | | | |
| Replication | 2 | 11.16 | 7.38* | 6.17 | 2.06 |
| Generations | 5 | 448.40*** | 316.35*** | 277.6** | (4)931.67*** |
| Error | 10 | 9.77 | 5.26 | 5.37 | 3.52 |
| CV | | 4.71 | 2.81 | 3.17 | 2.58 |
| Mean | | 66 | 64 | 73 | 70 |
| **Combined** | | | | | |
| Year | 1 | 18.77* | 2.77 | 5.28 | 2.52 |
| Replication (Year) | 4 | 12.1 | 13.1* | 5.27 | 2.23 |
| Generation | 5 | 926.51*** | 588.00*** | 433.77** | (4)1804.30*** |
| Error | 25 | 7.51 | (4)4.01 | 17.94 | 3.08 |
| CV (%) | | 4.12 | 3.11 | 5.89 | 2.48 |
| Mean | | 66 | 67 | 65 | 70 |

*, **, *** = significant at 5%, 1% and 0.01% probability; d=donor parent, r=recipient parent, CV= Coefficient of Variability

Considering the intra specie cross Var 19 ♂ × $Ab_2$♀, the $F_1$ hybrid mean was approximately intermediate between the donor and recipient parents for each and over the years (Table 3). In the cross Var 19 x $Ab_2$, days to flowering decreased from 70 d ($F_1$) to 62 d ($F_2$) and 71 d (F1) to 58 d ($F_2$). The $F_1$ hybrid means for days to flowering (70 d, 71 d and 71 d) did not equaled the means recorded in the $F_2$, $BC_1$ and $BC_2$. Days to flowering in the $F_2$ and $BC_2$ population means (62 d and 50 d) were closer to recipient parent (56 d), and less than the mid parent (69 d). In intra species cross Var 26♂ × Var 24♀, days to flowering in the $F_1$ hybrid averaged 67 days, this is lower than mid parent value (69 d), and larger than the recipient parent (57 d). Further, the $F_2$ population mean (57 d) though less than the mid parent value (69 d), skewed to the early flowering parent (57 d). The $F_1$ hybrid mean of intra specie cross MM 268 ♂ × MM 150 ♀ was close to the mid parent values (74 d, 73 d, and 74 d) for each year and pooled. The backcross generation ($BC_1$ and $BC_2$) means skewed to the early flowering parent (i.e less than the MP). In the cross Fovembot-2 ♂ × $DB_3$ ♀, the $F_1$ hybrid mean (77 d) almost equaled the mid-parent value (74 d).

**Table 3.** Quantitative trait data ± Standard Error, and individual scaling tests for five ($P_1$, $P_2$, $F_1$, $F_2$, $F_3$) and six ($P_1$, $P_2$, $F_1$, $F_2$, $F_3$, $BC_1$) generations for earliness in four cross combination in two years

| Cross | Year 1 | Year 2 | Combined |
|---|---|---|---|
| Var 19[d] | 82.00±0.39 | 82.00±1.90 | 82.00±0.31 |
| Ab2 [r] | 56.00±0.58 | 55.0±1.87 | 56.00±0.43 |
| $F_1$ | 70.33±0.38 | 71.00±2.34 | 71.00±0.37 |
| $F_2$ | 62.67±2.91 | 60.00±4.34 | 58.00±1.82 |
| $BC_1$ | 74.67±2.60 | 77.00±1.00 | 76.00±1.32 |
| $BC_2$ | 50.33±2.03 | 51.00±4.34 | 51.00±1.31 |
| MP | 69.00 | 69.00 | 69.00 |
| A | - 3.33±5.23 | 0.33±2.32 | -1.50±2.46 |
| B | -25.67±41.17 | -21.33±14.13 | -23.16±22.30 |
| C | -56.33±11.69** | -41.67±11.25** | -49.00±7.35** |
| D | -13.47±11.23 | -10.33±7.44 | -12.00±7.33 |
| m | 41.83±17.21** | 47.83±29.7 | 44.83±25.70 |
| h | 13.17±0.57** | 3.50±0.70* | 13.33±0.64** |
| h | 26.83±42.9 | 23.50±60.01 | 25.16±51.02 |
| $X^2$ | ** | ** | ** |
| Var 26 [d] | 80.00±1.15 | 83.00±2.70 | 82.00±2.27 |
| Var 24 [r] | 57.00±1.45 | 56.00±2.6 | 57.00±1.43 |
| $F_1$ | 67.00±1.20 | 59±2.52 | 60.00±1.94 |
| $F_2$ | 57.00±2.03 | 62±3.61 | 61.00±1.95 |
| $BC_1$ | 67.00±1.73 | 68±2.31 | 67.00±1.31 |
| $BC_2$ | 55.00±1.53 | 58.00±1.87 | 56.00±1.23 |
| MP | 69.99 | 70.00 | 70.00 |
| A | -16.00±3.90** | -16.33±3.00** | -16.16±3.95** |
| B | -7.00±6.59** | -14.000±9.00 | -10.83±11.87 |
| C | -19.00±11.66 | -19.67±14.18 | -19.33±11.21 |
| D | 2.00±1.00 | 5.67±3.00 | 3.83±16.31** |
| m | 73.50±18.4** | 80.83±16.9*** | 77.16±16.31** |
| d | 13.17±0.40 | 13.17±0.57** | 13.17±0.36*** |
| h | -35.83±41.7 | -58.17±35.87 | -47.00±36.8 |
| $X^2$ | ** | ** | ** |
| MM 268[d] | 85±0.67 | 85±0.66 | 85±0.20 |
| MM150 [r] | 63±0.57 | 62±0.57 | 63±0.11 |
| $F_1$ | 75±0.57 | 74±0.57 | 75±0.20 |
| $F_2$ | 70±1.52 | 78±1.15 | 74±2.07 |
| $BC_1$ | 74±1.15 | 72±1.15 | 73±0.73 |
| $BC_2$ | 63±0.88 | 62±0.81 | 63±0.24 |
| MP | 74 | 73 | 74 |
| A | -11.67±2.46** | -15.33±11.47 | -13.50±11.88 |
| B | -13.33±13.16 | -11.67±7.82 | -12.50±9.13 |
| C | -32.33±26.28 | 32.33±4.83** | -1.00±8.35 |
| D | -3.67±2.20 | 29.67±2.33** | 13.00±8.34 |
| m | 66.50±13.22** | 10.83± 2.21** | 99.83±37.08** |
| d | 133.17±21.23** | 11.17±3.33** | 11.17±0.68** |
| h | -9.17±4.54 | -145.50±101.32 | -77.33±77.11 |
| $X^2$ | ns | ** | ** |
| Fovembot-2 [d] | 96.0±0.57 | 88.0±0.57** | 97.0±0.42** |
| Db3 [r] | 57.0±0.67 | 58. 0±0.84 | 56.0±.43 |
| $F_1$ | 77.0±0.56 | 77.0±0.60 | 77.0±0.36 |
| $F_2$ | 68.0±0.88 | 64.0±1.83 | 66.0±1.08 |
| $F_3$ | 55.0±0.88 | 56.0±1.15 | 55.0±0.66 |
| MP | 76 | 72 | 76 |
| A | - | - | - |
| B | - | - | - |
| C | -35.66±3.99** | -52.67±6.29** | -44.16±5.67** |
| D | - | - | - |
| m | - | - | - |
| d | 20.17±0.57** | 20.67±0.91** | 20.42±0.73** |
| h | - | - | - |
| $X^2$ | ** | ** | ** |

*, **= significant at 5% and 1% probability; d=donor parent, r=recipient parent, MP= Mid Parent Value, m = mean, A, B, C and D = Individual Scaling test of Mather (1949)

The cross $Ab_2$ ♂ × Var 19 ♀ showed insignificant (P< 0.05) A, B and D – scale tests, and significant C (P<0.01) scale test for each year and combined (Table 2). In addition, significant (P<0.01 and 0.05) and Insignificant A, B, C and D scale tests were recorded in the cross Var 26 ♂ × Var 24 ♀, Fovembot-2 ♂ × $DB_3$ ♀ and MM 268 ♂ × MM 150 ♀ for each year and combined.

Over the years, the fit of the six parameter model in the cross Var 19 × $Ab_2$ showed positive and significant main effects ([a] + [d]) for each year and combined (Table 4). Additive and dominance genes were positive and significantly contributed to earliness for each year and combined. Interaction components [aa], [ad] and [dd] accounted for 25% of the total variation compared to the main effects ([a] + [d]) (35%) for combined data. Furthermore, the additive × additive digenic interaction [aa] and additive × dominance type of digenic interaction [ad] were positive and significant (P< 0.01) for each year and combined. In the cross $Ab_2$ ♂ × Var 19 ♀, dominance by dominance [dd] digenic effects were relatively low in magnitude, and statistically insignificant. Dominance × dominance digenic interaction [dd] appeared least important in the inheritance of earliness.

**Table 4.** Estimates of genetic effects for five or six generation means for four cross combinations fitted to 5 and 6 parameter model for earliness and estimates for heritability and heterosis in Arusha, Tanzania

| Var 19 × Ab2 | Year 1 | Year 2 | Combined |
|---|---|---|---|
| [m] | 62.67±8.45** | 60.00±1.25** | 57.67±1.82** |
| [a] | 24.33±1.88** | 24.33±2.55** | 24.30±1.56** |
| [d] | 25.53±7.09** | 23.88±9.11** | 26.11±5.67** |
| [aa] | 27.33±6.88** | 20.66±8.83** | 24.00±5.40** |
| [ad] | 11.16 ±2.21** | 10.8± 2.85** | 11.00±1.74** |
| [dd] | 1.66±10.33 | 0.33±13.2 | 1.00±8.10 |
| Hn (%) | 71 | 77 | 56 |
| AMPH | 1.17 | 2.50 | 2.00 |
| RMPH | 1.69 | 3.65 | 2.89 |
| AHPH | -12.00 | -11.00 | -11.00 |
| RHPH | -14.58 | -13.41 | -13.41 |
| N1 | 3.34 | 17.76 | 2.97 |
| N2 | 3.34 | 17.76 | 2.90 |
| Var 25 ×Var 24 | Year 1 | Year 2 | Combined |
| m | 57.33± 2.03 | 62.00±3.61 | 59.84±1.94 |
| [a] | 8.66±1.82** | 12.33±1.43** | 10.58±1.15** |
| [d] | -8.33±6.50** | -15.83±5.26** | -12.83±4.12** |
| [aa] | -4.00±6.33 | -11.33±5.10 | -7.66±4.06 |
| [ad] | -4.50±2.04 | -0.83±1.64 | -2.66±1.37 |
| [dd] | 27.00±9.50** | 42.33±7.56** | 34.67±6.00** |
| Hn (%) | 127 | 132 | 131 |
| AMPH | -19.00 | -10.05 | -7.77 |
| RMPH | -1.45 | -15.10 | -11.08 |
| AHPH | -12.33 | -23.67 | -19.67 |
| RHPH | -15.41 | -28.63 | -23.98 |
| N1 | 8.48 | 2.45 | 13.13 |
| N2 | 8.38 | 2.40 | 13.08 |
| MM 268 × MM 150 | Year 1 | Year 2 | Combined |
| [m] | 70.00±1.52 | 78.00±1.33 | 74.00±14.16 |
| [a] | 9.67±1.81** | 11.67±1.98** | 10.67±2.44** |
| [d] | -59.16±6.75** | 8.56±7.09 | -25.33±8.74** |
| [aa] | -59.33±6.32** | 7.33±6.80 | -26.80±8.43** |
| [ad] | -1.83±2.11 | 0.83±2.20 | -0.50±2.73 |
| [dd] | 86.33±9.82** | 17.67±10.32 | 52.0±12.7** |
| Hn (%) | 109 | 50 | 101 |
| AMPH | 1.00 | 1.00 | 1.00 |
| RHPH | 1.35 | 1.36 | 1.35 |
| AHPH | -10.00 | -11.00 | -10.20 |
| RHPH | -11.76 | -12.94 | -11.74 |
| N1 | 3.77 | 23.00 | 2.52 |
| N2 | 3.76 | 22.50 | 2.50 |
| Fovembot × $Db_3$ | Year 1 | Year 2 | Combined |
| [m] | 68.00±0.88 | 65.00±1.53 | 65.66±1.08 |
| [a] | 20.16± 0.45** | 20.66±0.63** | 20.11±1.04** |
| [d] | 18.0±1.82** | 26.00±2.53** | 22.0±1.90*** |
| [aa] | 17.83±1.51** | 26.33±2.10** | 22.08±1.64** |
| [ad] | - | - | - |
| [dd] | - | - | - |
| Hn (%) | - | - | - |
| AMPH | 1.00 | 5.00 | 1.00 |
| RMPH | 1.32 | 6.94 | 1.32 |
| AHPH | -19.00 | -11.00 | -20.00 |
| RHPH | -19.79 | -12.50 | -21.00 |
| N1 | 1.51 | 21.27 | 32.15 |
| N2 | 1.50 | 21.24 | 32.11 |

*, **,= significant at 5% and 1% probability, m = mean, [d] = additive, [h] = dominance, [i] = additive × additive dominance digenic interaction, [j] = additive × dominance digenic interaction, [l] = dominance x dominance digenic interaction, AMPH = Absolute mid parent heterosis, RMPH = Relative mid parent heterosis, AHPH = Absolute high parent heterosis, RHPH = Relative high parent heterosis, N1= Effective factors (Wright,1968), N2 = Effective factors (Cookerham, 1986)

A large phenotypic difference (days to flowering) between Var 26 ♂ and Var 24 ♀ account for significant and positive additive gene [a] compared to dominance gene [d] for each year and combined (Table 4). The main effects ([d + h]) are important in the genetic control of earliness compared to digenic interaction. Among the digenic interaction components, the additive by additive digenic [aa] and additive by dominance [ad] digenic interaction recorded insignificant (P>0.05) estimates, although estimates of dominance × dominance digenic interaction [dd] were significantly positive. Considering the cross MM 268 ♂ × MM 150 ♀, the fit of the six parameter model showed that additive gene [a] gene was positive and significant (P<0.01) for each year and combined data. Additive × additive [aa] digenic interaction and dominance by dominance digenic [dd] interaction recorded positive and significant (P<0.01) estimates for combined. In Fovembot-2 ♂ × $Db_3$ ♀, additive gene [a], dominance gene [d] and additive by additive [aa] digenic interaction were positive and significant (P< 0.01).

Heritability estimates in narrow sense were high in $Ab_2$ ♂ × Var 19♀. In the cross Fovembot-2 ♂ × $Db_3$ ♀, heritability estimates were greater than theoretical limits, i.e., 100% and more. This may be ascribed to sampling error, differential response of the $F_2$ population and backcross generations to the environment, and digenic epistatic action. The values of heterosis relative to mid parent (AMPH and RMPH) in the cross $Ab_2$ ♂ × Var 19♀, MM 268 ♂ × MM150 ♀ and Fovembot-2 ♂ × $Db_3$ ♀ were positive for individual year and combined. AHPH and RHPH recorded negative estimates for each year and combined. Hence hybrid vigour was low, and higher manifestation of the recipient parent (with shorter days to flowering) was evident. Negative estimates for AMPH, RMPH, AHPH and RHPH were recorded in the cross Var 26 ♂ × Var 24 ♀. The number of genes controlling earliness ranged from 3 to 32 genes for each year and combined for all the cross combinations.

## DISCUSSION

The individual scaling test of Mather (1949) and joint scaling test (Cavali, 1952) indicates an overwhelming evidence of interaction among multiple genes for earliness. Hence, the segregating population have to be forwarded to the next generation in order to arrive at the best fit model (Mather and Jinks, 1982). The generation means provided basis for selection of early, medium and late flowering types in the segregating population. In three cross combinations, the generation means among backcross generations lend weight to the fact that earliness gene was associative among the parents. Additive and dominance gene effects contributed significantly to earliness in intra species cross $Ab_2$ × Var 19 and inter species cross Fovembot-2 ♂ × $Db_3$ ♀. But dominance in direction of late flowering parent predominates. This indicates the possibility of developing medium flowering varieties after series of evaluation and selection. In contrast, additive effects governed inheritance of earliness compared to dominance gene in intraspecies cross Var 26 ♂ × Var 24 ♀ (*Solanum aethiopicum*) and MM 268 ♂ × MM 150 ♀ (*Solanum macrocarpon*). Dominance effects were negative and in direction of the early flowering parent. Negative sign of dominance [h] suggest that alleles from the males (Var 26 and MM 268) are recessive to alleles from the females (Var 124 and MM 150), and the parent with shorter days to flowering predominates in these cross combinations. With additive gene action for days to flowering, selection among segregating generation will develop early flowering and maturing varieties. Additive effects for days to flowering in this research agrees with results previously reported by Mittal

*et al.* (1976) which indicate additive effect for earliness in *Solanum melongena*. With additive gene for earliness, pure line selection followed by pedigree selection method will be effective to achieve generation progress.

In addition, dominance [d] gene effect favour early flowering in the cross Var 25 × Var 26 and MM 268 × MM 150. Dominance effects [h] for earliness presupposes that selection should be delayed until heterozygosity is reduced among the population through selfing. Genetic enhancement of earliness was obvious in the cross $Ab_2$ ♂ × Var 19 ♀ and Fovembot-2 ♂ × $Db_3$ ♀ due to positive and significant ($P<0.01$) additive × additive digenic interaction [aa]. Significantly negative additive × additive digenic interaction in the cross MM 268 × MM 150 suggest depression of earliness. Earliness was adequately explained by digenic epistatic model (dominance × dominance digenic interaction) in Var 25 × Var 26 and MM 268 × MM 150. Dominance in direction of early flowering along with positive dominance × dominance digenic interaction would indicate duplicate epistasis, which is undesirable in selection. Duplicate epistasis in two cross combinations indicates that variability in segregating generations may be reduced, which hinder improvement of earliness through selection (Chaudhary and Pathania, 2001). Selection should therefore be done in later generations to allow for fixation of earliness genes.

A large contributions of epistasis to earliness may have inflated the estimates of heritability in the cross Var 26 × Var 24 and MM 268 × MM 150. A preponderance of additive effects coupled with high narrow sense heritability for earliness in the cross $Ab_2$ ♂ × Var 19 ♀ indicates that selection may be effective in subsequent generation for earliness. In addition, early fruit types will be developed, if segregating populations are selected for genetic improvement. However, pedigree programmes could be worthwhile to advance improvement in earliness. It was possible that dominance and non-allelic interaction might have biased up the estimates of heritability. Considerable heterosis for earliness was associated with the superiority of the $F_1$ over the mid parent and sufficient divergence among the parents implied favourable situation for genetic improvement.

Four cross combinations (Var 19 ♂ × AB ♀$_2$, MM 268 ♂ × MM 150 ♀ and $DB_3$ ♂ × Fovembot-2 ♀) are promising for hybrids development. The presence of non-allelic interaction for these crosses may be associated with increase or decrease in expression of heterosis for earliness (Hayman, 1974). Considerable heterosis for earliness in bringal (*S. melongena*) had been reported (Kathiria and Sharma, 1996). The methods of estimating effective factors for earliness varied greatly. Effective factors for earliness indicated polygenic action, meaning that genotypes with stable performance could be developed. Furthermore, some cross combinations showed small number of effective factors, this seems to regulate earliness. Therefore fixation of earliness may be reached in few generations under high selection intensity. The estimates of epistasis as well as dominance and additive gene action may have been influenced by genotype by environment interaction in both five-parameter and six-parameter models. With dominance and non-allelic interaction for earliness in cross combinations investigated recurrent selection will be adequate to develop hybrids and open pollinated varieties.

## CONCLUSION

Analysis of generation mean was useful in understanding the mode of inheritance and genetic control of earliness in Scarlet, Gboma and *S. anguivi*. The lack of fit of the three-parameter model provided evidence of dominance and epistasis for

earliness. The five and six parameter models provided showed additive, dominance and epistatic effects for earliness in Scarlet, Gboma and *S. anguivi*. However, the kind and magnitude of genetic action (additive, dominance, duplicate epistasis and complementary epistasis) suggest a selection methods that will mop up several genetic actions. This investigation showed the possibility of developing early maturity types due to additive gene. Var 19 ♂ × AB ♀$_2$, MM 268 ♂ × MM 150 ♀ and DB$_3$ ♂ × Fovembot-2 ♀ are promising for hybrid development. The magnitude of heterosis obtained for some crosses indicated the possibility of development of early and extra early varieties from the accessions.

## REFERENCES


Adeniji, O.T., Kusolwa, P and Reuben, S.W.O.M. 2012. Genetic diversity among accessions of *Solanum aethiopicum* L. groups based on morpho-agronomic traits. *Plant Genetic Resources*, Available on CJO 2012 doi:10.1017/S1479262112000226

Adeniji, O.T. and Aloyce, A. 2012. Farmers' knowledge of horticultural traits among eggplant (Solanum spp) and development of new African eggplant varieties (*Solanum aethiopicum*) in Tanzania. *Tropicultura*. 30(3): 185-191

Adeniji, O.T. 2013. Morpho-agronomic and molecular diversity among seven relatives of the eggplant and inheritance of agronomic traits 321p.

Bartlett, M.S. 1937. Some examples of statistical methods of research in Agriculture and Applied Biology. *Journal of Research Statistics and Social Supplements* l4:137 - 183.

Bukenya, Z.R. and J.F. Carasco. 1994. Biosystematic study of *Solanum macrocarpon L. – S. dasyphyllum L.* complex in Uganda and relations with *Solanum linnaeanum*. *East African Agric. For. J* 59 (3): 187-204.

Bukenya, Z.R. 2004. *Solanum anguivi*. pp. 480 - 482. In: *Plant Resources of Tropical Africa 2.* (Edited Grubben, G.J.H. and Denton, O.A. eds.) PROTA Foundation, Wageningen, Netherlands/Blackhuys Publishers, Leiden Netherlands/CTA, Wageningen, Netherlands.

Cavalli, L. 1952. *An analysis of linkage in quantitative inheritance.* In: Reeve, E.C.R., Waddington, C.H. (eds.). pp 54.

Cockerham, C.C. 1986. Modifications in estimating the number of genes for quantitative character. *Genetics* 114: 659 – 684.

Collonnier, C., Fock, I., Kashyap, V., Rotino, G.L., Daunay, M.C., Lian, Y., Mariska, I.K., Rajam, M.V., Servaes, A., Ducreux, G. and Sihachakr, D. (2001). Applications of Biotechnology in eggplant. *Plant Cell, Tissue and Organ Culture* 65:91-107

Chaudhary, D.R. and Pathania, N.K. 2001. Inheritance of agronomical and physiological growth parameters in brinjal (*Solanum melongena L.*). *Himachal Journal of Agricultural Research.* 26 (1–2): 62–66.

Daunay M.C., Lester, R.N. and Ano, G. 2001. Cultivated eggplants. pp. 200 – 225. In: *Charrirer, A, Jacquot, M, Hamon, S. and Nicholas, D.* (eds.) *Tropical Plant Breeding*. Oxford University Press, Oxford.

Gamble E.E. 1968. Gene effects in corn I: Separation and relative importance of gene effects for yield. *Canadian Journal of Plant Science* 15: 77-78.

Kashyap, V., Kumar, S.V., Collonnier, C., Fusari, F., Haicour, R., Rotino, G.L., Sihachakr, D. and Rajam, M.V. 2003. Biotechnology of eggplant. *Scientia Horticulture* 97:1-25.

Hayman, B.I. 1974. The separation of epistatic from additive and dominance variation in generation mean. *Heredity* 12: 371 - 390.

Kathiria, K.B. and Sharma, R. K. 1996. Genetic analysis for earliness, plant height and kernel weight in two bread wheat crosses under normal and saline sodic soils. *Indian Journal of Genetics* 56: 548 - 552.

Kearsey, M.J. and Pooni, H.S. 1996. *The Genetic Analysis of Quantitative Traits*. Chapman and Hall, London. 456p.

Lester, R.N. and Hawkes, J.G. 2001. *Solanaceae*. In: Mansfed's encyclopedia of agricultural and horticultural crops (Hanelt). Springer-Verlag, Berlin. pp. 1790–1856.

Lester, R.N. and Daunay, M.C. 2003. Diversity of African Vegetable Solanum species and its implications for a better understanding of plant domestication pp.137–152. In: Knüpffer, H. and Ochsmann, J. (eds.) *Rudolf Mansfeld and Plant Genetic Resources*).Schriften zu Genetischen Ressourcen (DEU).

Mather, S.K. 1949. *Biometrical Genetics: The Study of Continuous Variation*. Dover Publications. Inc. London. 356pp.

Mather, K. and Jinks, J.L. 1982. *Biometrical genetics*. 3rd edition. Chapman & Hall, London, 396 pp.

Mittal, R.K., Singh, S.N. and Singh, N. N. 1976. Genetics of some characters in brinjal (*S. melongena*) and its wild relatives *S. turvum*. *South West Journal of International Cooperation* 2: 96 - 106.

Omidiji, M.O. 1979. Crossability relationships between some species of *Solanum lycopersicum* and Capsicum cultivated in Nigeria. pp. 605 – 614. In: Hawks, S.G., Lester, R.N. and Skewing, A.D. (eds.). *The Biology and Taxonomy of Solanaceae*) London Academic Press.

SAS STAT Software 9.12. Release 2009 Copyright (c) by SAS Institute Inc., Cary, NC, USA.

Schippers, R.R. 2002. *African Indigenous Vegetables*: An overview of the cultivated species 2002 Revised Version on CD-ROM. Natural Resources Institute, Chatham, United Kingdom. 214pp.

Warner, J.N. 1952. A method for estimating heritability. *Agronomy Journal* 44:427–430.

Wright, S. 1968. *Evolution and Use of Population Genetics.* Genetic and Biometrics Foundation, University of Chicago Press. 469pp.