Research Application Summary

Mode of gene action in inheritance of vegetative, floral and leaf yield traits in the African eggplant (*Solanum aethiopicum*)

Buteme, R.,[1*] Kabod, P.N.[1], Sseremba, G. [1,2,] & Kizito, E. B.[1]

[1]Department of Agricultural and Biological Sciences, Faculty of Agricultural Sciences, P.O.Box 4, Uganda Christian University, Mukono, Uganda
[2]National Agricultural Research Organization-NACORRI, P. O. Box 185, Kituza, Mukono, Uganda
Corresponding Author: ruthbuteme@gmail.com

Abstract

Understanding gene actions and how they contribute in the expression of characters is of great importance when devising an efficient selection program through the use of a suitable mating design. This study sought to determine the mode of gene action involved in inheritance of vegetative and floral traits in *Solanum aethiopicum*. Specifically, to establish probable existence of dominance and combining ability of the studied *S. aethiopicum* genotypes. To do this, twenty-nine (29) successful hybrids from a partial diallel crossing design along with their parental lines were evaluated to determine the mode of gene action involved in inheritance of vegetative, floral and leaf yield traits of *S. aethiopicum*. A multivariate linear mixed model fit by REML was used to estimate variance components for general combining ability (GCA) and specific combining ability (SCA) in the incomplete diallele design. The specific combining ability (SCA) effects were significant (p>0.01) for all traits measured at 6 and 8 weeks after planting (WAP) except for Harvest Index. Broad-sense heritability (H^2) values were generally high (>80%) for all traits compared to narrow sense heritability (h^2) at both stages of harvest; moreover Baker's ratio for these traits was low. The estimates of dominance variance were also higher in magnitude than corresponding estimates of additive variance. The cross N2xN14 had the highest SCA effects for majority of the vegetative traits and floral traits at both 6 and 8WAP. The results showed that non-additive gene action (dominant, additive dominant and dominant dominant effects) takes centre stage in inheritance of petal colour, stem colour, relative style length, stem hairiness, plant height, number of leaves, plant canopy width, and stem girth, flowers per inflorescence and flowers per plant and harvest index. However, inheritance of leaf area is governed by additive gene action. Therefore, for improvement of the African eggplant, methods such as restricted recurrent selection in early segregating generations might be appropriate.

Key words: Combining ability, diallel, gene action, *Solanum aethiopicum*

Résumé

Comprendre les actions des gènes et comment ils contribuent à l'expression des caractères est d'une grande importance lors de la conception d'un programme de sélection efficace grâce à l'utilisation d'une conception d'accouplement appropriée. Cette étude visait à déterminer le mode d'action des gènes impliqués dans l'hérédité des traits végétatifs et floraux chez Solanum aethiopicum. Plus précisément, pour établir l'existence probable de la dominance et de la capacité de combinaison des génotypes de S. aethiopicum étudiés. Pour ce faire, vingt-neuf (29) hybrides réussis issus d'un modèle de croisement diallèle partiel ainsi que leurs lignées parentales ont été évalués pour déterminer le mode d'action des gènes impliqué dans l'hérédité des traits de rendement végétatif,

floral et foliaire de S. aethiopicum. Un ajustement de modèle mixte linéaire multivarié par REML a été utilisé pour estimer les composantes de variance pour la capacité de combinaison générale (CCG) et la capacité de combinaison spécifique (CCS) dans la conception diallèle incomplète. Les effets de la capacité de combinaison spécifique (CCS) étaient significatifs (p>0,01) pour tous les caractères mesurés à 6 et 8 semaines après la plantation (WAP), à l'exception de l'indice de récolte. Les valeurs d'héritabilité au sens large (H2) étaient généralement élevées (> 80 %) pour tous les caractères par rapport à l'héritabilité au sens étroit (h2) aux deux stades de la récolte ; de plus, le ratio de Baker pour ces traits était faible. Les estimations de la variance de dominance étaient également plus élevées que les estimations correspondantes de la variance additive. Le croisement N2xN14 a eu les effets CCS les plus élevés pour la majorité des traits végétatifs et des traits floraux à 6 et 8WAP. Les résultats ont montré que l'action génique non additive (effets dominants, additifs dominants et dominants x dominants) occupe une place centrale dans l'héritage de la couleur des pétales, de la couleur de la tige, de la longueur relative du style, de la pilosité de la tige, de la hauteur de la plante, du nombre de feuilles, de la largeur du couvert végétal, et circonférence de la tige, fleurs par inflorescence et fleurs par plante et indice de récolte. Cependant, l'hérédité de la surface foliaire est régie par l'action additive des gènes. Par conséquent, pour l'amélioration de l'aubergine africaine, des méthodes telles que la sélection récurrente restreinte dans les premières générations en ségrégation pourraient être appropriées.

Mots clés : Capacité de combinaison, diallèle, action des gènes, Solanum aethiopicum

Introduction

Solanum aethiopicum also known as the Ethiopian eggplant, Ethiopian nightshade, Bitter tomato, African eggplant or Scarlet eggplant is a herbaceous vegetable belonging to section Oliganthes, sub family Solanoideae, family Solanaceae (Adeniji *et al*., 2012). Two out of the four-cultivar groups of the *S. aethiopicum* complex are commonly grown and consumed in several parts of Sub-Saharan Africa. Particularly in Uganda, *S. aethiopicum* is grown for its leaves (Shum group) and fruit (Gilo group) (Pincus, 2015). The crop is nutrient-rich and has a wide range of genetic and morphological diversity (Sseremba *et al*., 2017). Widely, *Solanum aethiopicum* is described as a shrub, perennial or annual herb, up to 200 cm tall; often much branched with or without prickles and stellate hairs on the branches and leaves (Lester and Seck, 2004). *Solanum aethiopicum* takes 5-8 weeks to start flowering and corolla are white, sometimes pale purple; the style is as long as or slightly longer than stamens, with a small obtuse stigma (Lester and Seck, 2004). The *Solanum aethiopicum* Shum group is harvested at 6 to 8 weeks after planting while the fruit in the Gilo group, a perennial, is harvested beginning at 8 weeks and can go on until fruiting is suppressed (Onyegbule *et al*., 2018). *Solanum aethiopicum* Shum cultivars can yield up to 225 t ha^{-1} (Nanyanzi *et al*., 2018) and 150 t per hectare for Gilo (Onyegbule *et al*., 2018). However, various biotic and abiotic stresses cause fluctuation in these yield potentials (Sseremba *et al*., 2018). There is need for varieties of *S. aethiopicum* that can produce satisfactory yields sustainably to meet the growing demand for this vegetable throughout the year; over 200t of the crop are demanded weekly in Ugandan markets alone (Jagwe *et al*., 2016).

Solanum aethiopicum is indigenous to Africa and the considerable genetic variation can be exploited to produce superior varieties for yield and resistance to abiotic and biotic stresses. As much as *S. aethiopicum* is a common and important crop in Sub Saharan Africa, compared to other solanaceous crops such as *S. melongena*, *S. tuberosum, S. lycopersicum*, etc., there are limited improvement efforts especially in hybrid development. As such, there is inadequate information

on the nature and magnitude of genetic parameters controlling the inheritance of desirable traits that would support a breeding program. *Solanum aethiopicum* breeding focuses on improving leaf and/or fruit biomass and morphological markers such as leaf, stem and flower traits can be used in discrimination of true hybrids. Patterns of inheritance of these morphological markers are viable indicators of the mode of gene action. Studies in Amaranthus (Reddy and Varalakshmi, 1998), *Spinacia oleracea* (Thakur and Verma, 2000) and *S. melongena* (Kumar, 2013) show the importance of non-additive gene action in inheritance of leaf and fruit traits. In *S. aethiopicum*, non-additive gene action was prominent in the inheritance of leaf yield attributes in drought conditions (Sseremba, 2019).

Estimation of gene action for such morphological traits can enable breeders to gain understanding of their breeding material. Combining ability variances have been used to measure gene action using mating designs such as the diallele (full or partial) and North Carolina (NCI, NCII and NCIII) (Bu *et al.*, 2015). In these studies, information generated on general and specific combining ability has been used to identify superior individuals to be used as parents for hybridization and indicate cross combinations likely to yield desirable segregates (Hussain *et al.*, 2017). In this study, it was hypothesized that non-additive gene action was not only responsible for inheritance of leaf yield traits but also other vegetative and floral traits in *S. aethiopicum*. This study therefore sought to determine the mode of gene action involved in inheritance of vegetative and floral traits in *S. aethiopicum*. Specifically, to establish probable existence of dominance and combining ability of the studied *S. aethiopicum* genotypes.

Materials and Methods

The experiment was set up at the Department of Agricultural and Biological Sciences at Uganda Christian University. Uganda Christian University is located in Mukono (0 21'27.0"N, 32 44'29.0"E; Latitude: 0.357500; Longitude: 32.741389) approximately 22 kilometers east of Uganda's capital city, Kampala.

Seven (7) breeding lines at the S4 generation from Uganda Christian University (UCU) seed bank were used as parents in this study. See Table 1 for details.

Table 1. Description of the genotypes used in the study

Genotype Code	Species	Pedigree	Petal colour	Style length (cm)	Stem colour	Leaf hairs	Plant height (cm)
N2	*S. aethiopicum Shum*	SAS183/G/2015	White	0.6	Green	Glaborous	32
N4	*S. aethiopicum Shum*	SAS163/G/2015	White	0.5	Green	Glaborous	31
N11	*S. aethiopicum Shum*	SAS148/2015	White	0.6	Green	Glaborous	45
N14	*S. aethiopicum Shum*	SAS184/G/2015	White	0.6	Green	Glaborous	33
N15	*S. aethiopicum Shum*	SAS137/2015	White-Purple	0.5	Purple	Glaborous	25
N18	*S. aethiopicum Shum*	SAS108/P/2015	White-Purple	0.6	Purple	Glaborous	63
G10	*S. aethiopicum Gilo*	SAG303/2015	White	0.7	Purple	Dense	32

Twenty-nine (29) successful hybrids from a partial diallel crossing design were used in the study. The diallel crossing design was used to estimate combining ability and further explore the veracity of maternal and paternal effects in the inheritance of traits (Sprague and Tatum, 1942; Griffings 1956). The F_1 seed, along with the parental lines (7) were evaluated in the field in 2019A (march-June) using a randomized complete block design with three replicates, 20 plants per plot.

Data collection and analysis. Thirteen (13) traits were measured on the Shum crosses data (Table 2) were collected at 6 and 8 weeks after planting (WAP) for vegetative traits while flowering data were collected between 7 and 9 WAP during full blossom. Genstat version 18 was used to generate descriptive statistics and inferential statistics. A chi-square analysis was done to test goodness-of-fit to appropriate Mendelian ratios at F1. The assumption here was that the vegetative and floral traits in *S. aethiopicum* follow a simple Mendelian pattern of inheritance. Further, that the purple colour and hairiness are a dominant trait as observed in *S. melongena* (Duanay *et al*., 2004).

To estimate variance components for general combining ability (GCA) and specific combining ability (SCA) in the incomplete diallele design, a multivariate linear mixed model fit by REML, general form $y = X\beta + Zu + \varepsilon$ provided in R sommer package (Covarrubias-Pazaran, 2016) was used. Where y is the measured phenotype, X is the incidence matrix for fixed effects like grand mean [μ], Z is the incidence matrix for random effects like GCA and SCA, β is the vector for BLUEs, u is the vector for BLUPs, and ε stands for residuals or environmental variance, (V_E) (Bu *et al*., 2015; Covarrubias-Pazaran, 2016). The BLUEs and BLUPs refer to best linear unbiased estimates of fixed effects and best linear unbiased predictions of random effects, respectively.

As example leaf yield data taken on the plants were predicted as follows: $y = X\beta + Z_u\,GCAmales + Z_u\,GCAfemales + Z_u\,SCA + \varepsilon$. Where y was the observed phenotype (Number of leaves per plant, Leaf size/area, Harvest index), X was the matrix for fixed effects (μ, blocks) and Z was the incidence matrix for random effects (GCAmales, GCAfemales and SCA).

Table 2. List of traits and how they were measured

S/N	Trait	Scale/Units
1	Plant height	Measured in centimetres (cm)
2	Number of leaves per plant	Counted number of marketable leaves per plant
3	Leaf size/Area	Measured in centimetres (cm)
4	Presence of leaf hairs on leaves	1= Glaborous, 2 = Hairy
5	Stem girth	Measured in centimetres (cm)
6	Stem colour	1= Green, 3= green purple, 5= purple
7	Petal colour	3-white; 5-purple; 7
8	Relative style length	3 = Short (~0.2cm) 5 = Intermediate (~0.4cm) 7 = Long (~0.5cm and above)
9	Number of flowers per inflorescence	Counted number of flowers per inflorescence from 10 inflorescence per plant
10	Number of flowers per plant	Counted number of flowers per plant
11	Economic yield	Weight of leaves from 10 plants per plot (Measured in grams (kg))
12	Biological yield	Weight of whole plant-shoot and leaves from 10 plants per plot (Measured in grams (kg))
13	Harvest Index (%)	Economic yield divided by Biological yield multiplied by 100

To decide on levels of significance of GCA and SCA effects, a 5 % error margin was used and subsequent estimates for variance components were conducted following Falconer and Mackay (1996) and Kang (2002). The decision on significance of combining ability effects was made basing on critical values of Z-ratio; 1.64, 2.33 and 3.09 (Bu *et al*., 2015; Covarrubias-Pazaran, 2016) for probability of difference by chance (α) being set at 0.05, 0.01 and 0.001, respectively. The GCA and SCA variance estimates were generated and used to calculate additive (V_A) and dominance genetic variance (V_D), respectively as follows: $V_A = 4 * V_{GCA}$ and $V_D = 4* V_{SCA}$ where $V_{GCA} = V_{GCA\,males} + V_{GCA\,females}$. Genotypic variance ($V_G$) was calculated as follows: $V_G = V_A + V_D$. The measured or phenotypic variance (V_P) was then estimated as: $V_P = V_A + V_D + V_{E/n}$; on the assumption of negligible epistatic effects (Falconer and Mackay, 1996; Kang, 2002), to facilitate the calculation of heritability.

General combining ability of parents and crosses were calculated by considering missing crosses as missing data using Excel (Falconer and Mackay, 1996; Kang, 2002). The following formulae were applied in Excel.

I. GCAmales= Mean performance of progeny of a given male – Mean of progeny from all males
II. GCAfemales = Mean performance of progeny of a given female – Mean of progeny from all females
III. SCAeffect= Observed mean of a cross – Expected mean of the cross
IV. Expected mean of cross = Overall mean (μ) + GCA for a given male + GCA for a given female
The broad sense heritability (H^2) and narrow-sense heritability (h^2) were calculated as follows: $H^2 = V_G / V_P$ and $h^2 = V_A / V$

Results and Discussion

Inheritance of qualitative traits (petal colour, stem colour, leaf hairiness and relative style length). The chi-square analysis showed no significant difference for expected and observed frequencies in the F_1 hybrids for petal colour, stem colour and leaf hairiness. The key petal characteristics observed in this study were either white-purple petals or white petals. All combinations (2) where both parents had white-purple petals produced offspring with white-purple petals. Six out of 14 combinations that involved a parent with white-purple petals and the other with white petals produced all their offspring with white-purple petals. Each of the remaining 8 combinations produced an average of 10 out of 180 flowers with white petals. The difference in the number of observed offspring with white-purple petals and those expected was not significant (p>0.05). The combinations where all parents had white petals, produced offspring with white petals. In terms of stem colour, when parents with purple stems were crossed with parents with green stems, all offspring inherited the purple stem colour. Combinations where all parents had green stems resulted in all green stem offspring and combinations where all parents had purple stems resulted in all purple stem offspring. On the other hand, for leaf hairiness, when parents with hairy leaves were crossed with parents with glaborous leaves, all offspring inherited the hairy leaf trait. Combinations where all parents had hairy leaves resulted in all hairy leafed offspring and combinations where all parents had glaborous leaves resulted in offspring with glaborous leaves.

In Mendel's experiments, he discovered that in a cross between parents displaying two contrasting traits, the hybrid (F_1) expressed one of the traits to the exclusion of the other. Mendel called the

expressed trait dominant and the suppressed trait recessive (Acquaah, 2012). In the present study, the colour purple was dominant over white in petals and over green in stems, pointing towards, non-additive/dominance gene action at play in inheritance these traits. These results are similar to those by Lin *et al.* (2006) and Pandiyan *et al*. (2020) where the same trait was found to have a dominant genetic control in *S. melongena* a close relative to *S. aethiopicum*. The inheritance of the white petal colour in over 50% of the combinations involving a white-purple petaled parent and a white petaled parent could be due to epistasis or selfing. An analysis of the same hybrids at F_2 would be appropriate to decipher what kind of epistasis may be at play. It is possible that petal colour in Shum might be di-allelic; hence the white-purple petal colour expression in parents.

All parents involved in the study had long styles (above 0.5cm with only a 0.1cm deviation). All hybrids inherited the long style trait. The inheritance of tristyly is generally thought to be governed by two diallelic loci, S and M, with complete dominance and epistasis between the loci (Lewis and Jones, 1992). A dominant allele at the S locus results in expression of the short-styled morph (S morph), whereas dominant alleles at the M locus and recessive alleles at the S locus (ssMm or ssMM) give rise to plants of the mid-styled morph (M morph). Recessive alleles at both loci (ssmm) lead to expression of the long-styled morph (L morph). All parents in this study had long styles resulting into off spring with only long styles indicating the presence of recessive long style genes (ssmm) in *Solanum aethiopicum*.

Inheritance of quantitative traits
General combining ability and specific combining ability. The analysis of variance for combining ability revealed that the variances for General Combining Ability (GCA) variances for all traits at both 6 and 8 WAP were not significant (p>0.01). However, Specific Combining Ability (SCA) variances were highly significant (p>0.01) for all traits measured at 6 WAP and for all traits measured at 8WAP except for Harvest Index (Table 3). In addition, the SCA variances were higher than the GCA variances for all traits at both stages except for leaf area at 8 WAP.

The variation in the GCA and SCA variances among traits indicate that considerable differences exist among them in the gene action. As such, the traits with higher SCA variances like those observed in this study exhibit non-additive (i.e., dominant, additive dominant and dominant dominant effects) genetic control (Fasahat *et al.*, 2016). The SCA variances are expected to be high in inbreeding populations (Kumar *et al*., 2020). Predominance of SCA other than GCA variances also indicates potential for hybrid vigour and that particular combinations with strong SCA will enable the production of *S. aethiopicum* lines with improved traits (Sseremba, 2019).

The GCA variance being higher than the SCA despite the SCA variance being significant for the leaf area trait indicates that both additive and non-additive effects are important in the inheritance of this trait (Acquaah, 2012). This result is also supported by the non-significant difference identified in the parent vs cross contrast for this trait. This suggests that breeding for leaf size will require parents with good GCA values, but also specific hybrid combinations. Maternal effects were high for all traits at all the stages except leaf area at 8 WAP. Genes carried in the maternal cytoplasm influence the hybrid phenotype and can therefore be tracked easily during crop improvement (Sseremba, 2019).

Table 3. Mean squares for GCA and SCA effects for measured traits at 6 and 8 Weeks after planting (WAP)

Trait	Source of variation	6 WAP	8 WAP
PH	GCA Females	49.13	36.7
	GCA Males	25.1	0
	SCA	147.97**	491.1**
	Residual	24.47***	231.6***
LPP	GCA Females	4.5	13.75
	GCA Males	1.84 0	
	SCA	6.06**	164.46***
	Residual	6.91***	94.36***
LA	GCA Females	1873	1394
	GCA Males	1550	2010
	SCA	3977***	1748**
	Residual	3596***	2419***
PC	GCA Females	16.04 2.261	
	GCA Males	7.12 0	
	SCA	53.64***	30.81***
	Residual	34.83***	26.7***
STG	GCA Females	0.04 0.033	
	GCA Males	0.0020.009	
	SCA	0.14***	0.1***
	Residual	0.12***	0.189***
FPI	GCA Females		0
	GCA Males		0
	SCA		10.213***
	Residual		4.849***
FPP	GCA Females		0
	GCA Males		0
	SCA		14232***
	Residual		7627***
HI	GCA Females		5.1
	GCA Males		0
	SCA		16.1
	Residual		35.43**

, *, Significant at 5% and 1% respectively. PH, plant height; LPP, leaves per plant; LA, leaf area: PC, plant canopy width; STG, stem girth; FPI, flowers per inflorescence; FPP, flowers per plant; EY, economic yield; BY, biological yield; HI, harvest index.

SCA Effects. At 6 WAP, N2xN14 had the highest specific combining ability effect for plant height, followed by N14xN15, N18xN11 and N11xN18 (Table 4) while N11xN14 had the lowest specific combining ability effect for this trait followed by N2xN18. For leaves per plant, N2xN14 had the highest specific combining ability effect followed by N18xN15 and N15xN4 while N2xG10 had the lowest SCA effect for this trait followed by N11xN14. For leaf area, N2xN14 had the highest SCA effect followed by N4xN11, N14xN4 and N11xG10 while N2xG10 had the lowest SCA effect

for this trait followed by N11xN14. In regards to plant canopy width, N2xN14 had the highest SCA effect while N11xN14 had the lowest followed by N4xN11. For stem girth, N2xN14 had the highest SCA effect for this trait followed by N4xN2 and N4xN11 while N2xG10 had the lowest SCA effect for this trait. Also N2xN14 had high and positive specific combining ability effects for all traits at 6 WAP (Table 4). At 8 WAP, N2xN14 exhibited the highest specific combining ability effect for plant height while N4xN15 displayed the lowest specific combining ability effect for this trait (Table 5). For leaves per plant, N4xN15 had the highest specific combining ability effect followed by N2xN14 while N18xN14 had the lowest SCA effect for this trait followed by N14xN4 and N18xG10. For leaf area, N4xN11 had the highest SCA effect followed by N2xN14, N4xN15 and N15xN4 while N2xG10 had the lowest SCA effect for this trait followed by N11xN14. In regards to plant canopy width, N4xN15 had the highest SCA effect followed by N2xN14, while N2xG10 had the lowest SCA effect for this trait followed by N11xG10. For stem girth, N11xN15 had the highest SCA effect for this trait followed by N11xN18 while N18xN14 had the lowest SCA effect for this trait. In regards to floral traits, N18xN11 had the highest SCA effects for flowerers per inflorescence and flowers per plant followed by N2xN14, N2xN11 had the lowest SCA effects for these traits. For harvest index, N18xN15 had the highest SCA effect for harvest index while the lowest SCA effect for this trait was observed in N18xG10 (Table 5). At 8 WAP, a similar trend to that at 6 WAP was observed, where N2xN14 had the highest SCA effects for majority of the vegetative traits and in this case, floral traits as well.

Specific combining ability reveals the best combination of crosses for the development of hybrids with desired traits. Hybrids with positive SCA effect values for leaf area and number of leaves maybe good indicators of a combination for high yielding Shum. Furthermore, the high number of flowers per plant is also an indicator of high fruit yield which would then result into high seed yield and therefore fostering further multiplication and conservation of genetic variability. In a study by Nakyewa *et al*. (2020), farmers preferred *Solanum aethiopicum* genotypes with high leaf and seed yield.

GCA Effects. Looking at the GCA effects at 6 WAP (Table 6), among the female parents, N11 and N18 exhibited high positive GCA effects for all traits, while G10 had the highest positive GCA effects for, leaf area, plant canopy width and stem girth. N14 had positive GCA effects for only three traits, leaf area, plant canopy width and stem girth. On the other hand, N2 and N4 presented with negative GCA effects for all traits. Among the males G10 exhibited the highest GCA effects for leaf area, plant canopy width and stem girth. N14 had positive GCA effects for plant height, leaf area and plant canopy width, N18 had the highest GCA effects for plant height and had positive GCA effects for leaves per plant and plant canopy as well. N2 had the highest GCA effect for leaves per plant, with positive GCA effects for plant canopy width. In general, G10 had positive GCA effects for all traits while N15, N4 and N11 had the lowest GCA effects for all traits. In regards to GCA effects at 8 WAP (Table 7), among the female parents, N18 and N11 exhibited high positive GCA effects for majority of the traits measured at this stage. Further, N18 had the highest GCA effects for plant height, leaves per plant, flowers per inflorescence and harvest index. G10 on the other hand, had the highest positive GCA effects for leaf area, plant canopy width and stem girth. N15 had the highest GCA effect for flowers per plant. Just as at 6 WAP, N2 and N4 presented with negative GCA effects for majority of the traits. Among the males, N11 had the highest GCA effects for plant height, stem girth and flowers per inflorescence. G10 had the highest positive GCA effects for leaf area and plant canopy width, N2 had the highest GCA effect

for flowers per plant In general, N11 and N14 had high positive GCA effects for majority of the traits while N15 had the lowest GCA effects for majority of the traits.

The high GCA effect values that were observed in N11, N18 and G10 for the measured traits at both 6 and 8 WAP show that these parents have the potential to transfer some of their traits to their offspring. It also indicates that for these traits, obtaining good hybrids require specific combinations of parents (Acquaah, 2012).

Table 4. Specific combining ability effects for traits measured at six weeks after planting

F1 Hybrid	PH	LPP	LA	PC	STG
N11xG10	3.1	1.0	75.1	-2.4	0.4
N11xN14	-23.6	-3.9	-126.5	-13.5	-0.3
N11xN15	0.5	1.2	48.7	6.1	0.1
N11xN18	12.3	0.9	-39.3	1.4	-0.2
N11xN2	4.5	1.0	-8.3	-0.8	-0.3
N11xN4	-4.4	0.3	-33.2	-1.0	-0.2
N14xN15	15.3	1.8	14.9	5.1	0.2
N14xN2	3.1	-0.3	39.1	1.4	0.0
N14xN4	4.9	-0.7	75.6	4.4	0.3
N15xN11	-1.0	-0.7	33.4	3.1	0.3
N15xN14	-6.8	0.9	-10.2	-7.5	0.1
N15xN18	-2.9	1.6	41.6	0.2	-0.2
N15xN2	-0.4	-1.1	7.8	1.4	0.1
N15xN4	10.1	2.8	10.0	2.8	0.0
N18xG10	-13.7	-0.1	-80.1	-5.4	-0.4
N18xN11	13.5	2.5	52.0	2.2	-0.1
N18xN14	9.3	0.0	58.9	2.2	0.4
N18xN15	-6.0	3.4	18.1	2.9	0.1
N18xN2	-10.8	-2.7	-63.9	-5.7	-0.3
N2xG10	4.7	-4.0	-130.3	-5.9	-0.9
N2xN11	-14.2	-1.0	-72.1	-14.3	-0.4
N2xN14	30.3	5.5	140.7	22.1	0.7
N2xN15	-0.3	-0.7	-12.8	-1.2	0.2
N2xN18	-18.2	-1.7	10.2	-3.5	0.2
N2xN4	-2.7	-1.8	4.5	-0.3	-0.1
N4xN11	10.8	-0.1	78.5	11.3	0.5
N4xN14	-1.6	-0.3	-3.5	0.8	-0.4
N4xN15	-6.4	-2.3	-23.9	-8.7	-0.4
N4xN2	3.6	1.4	25.3	4.1	0.6

PH, plant height; LPP, leaves per plant; LA, leaf area: PC, plant canopy width; STG, stem girth

Table 5. Specific combining ability effects for traits measured at eight weeks after planting

F_1 Hybrid	PH	LPP	LA	PC	STG	FPI	FPP	HI
N11xG10	-30.06	-12.31	29.84	-10.20	-0.33	-0.01	-41.1	3.52
N11xN14	-23.14	3.12	-64.57	-0.04	-0.25	-0.32	-80.2	-3.78
N11xN15	21.80	7.71	16.49	5.20	4.87	-3.64	-30.1	-5.40
N11xN18	11.10	2.74	-35.57	3.87	4.09	0.68	-62.7	-0.99
N11xN2	-12.78	-7.15	-17.00	-6.65	-0.31	1.88	116.7	6.19
N11xN4	8.08	9.74	-11.81	2.60	-0.09	3.58	147.9	-1.87
N14xN15	12.04	30.02	60.84	4.70	-0.18	4.23	101.8	-1.92
N14xN2	13.83	-7.81	55.25	-0.25	0.23	-2.36	-82.4	0.41
N14xN4	-4.17	-14.44	-40.46	-0.21	0.04	-1.26	-4.1	2.75
N15xN11	-5.51	-1.06	-32.75	-0.14	-0.23	-3.54	-117.7	1.56
N15xN14	-6.60	4.46	15.05	5.95	0.10	-0.84	-77.3	-2.71
N15xN18	-28.16	-8.62	-1.05	-10.10	0.07	3.72	-68.6	1.65
N15xN2	-1.42	7.78	13.72	2.02	-0.03	0.94	52.7	0.12
N15xN4	25.97	7.83	61.81	-0.27	-0.30	1.64	53.1	4.27
N18xG10	25.82	23.07	-59.59	4.52	0.07	2.53	19.1	-7.97
N18xN11	9.89	7.07	54.91	5.13	0.29	8.33	360	-4.95
N18xN14	-29.40	-22.34	-35.10	-9.75	-0.58	-1.96	-119.1	6.68
N18xN15	-7.98	-2.74	9.77	-2.82	-0.01	-1.70	-111.8	7.50
N18xN2	5.93	-2.47	-22.32	1.75	-0.10	-4.38	-119.9	-2.93
N2xG10	4.52	-8.05	-50.24	-11.68	-0.37	-1.28	17.1	0.84
N2xN11	-29.23	-6.49	-45.74	-4.59	-0.56	-4.82	-167.6	-0.05
N2xN14	54.55	25.21	69.65	7.25	0.45	3.49	216.8	-0.06
N2xN15	-7.55	-6.81	-28.78	-1.10	0.07	2.25	-12.5	-6.78
N2xN18	9.39	3.98	34.05	4.35	0.33	-2.34	4.6	-3.10
N2xN4	-16.92	-3.51	35.02	1.28	-0.28	-2.23	-112.1	4.74
N4xN11	22.03	2.15	75.90	3.82	0.16	1.32	-45.4	-7.60
N4xN15	-64.10	4.09	62.06	7.67	0.34	-0.51	-12.4	-0.42
N4xN2	3.70	6.90	31.16	4.00	0.02	-2.00	-53.9	-3.40

PH, plant height; LPP, leaves per plant; LA, leaf area: PC, plant canopy width; STG, stem girth; HI, harvest index

Table 6. General combining ability effects for traits measured at six weeks after planting

GCA Effects	PH	LPP	LA	PC	STG
Female G10	-8.2	0.7	138.5	10.5	0.7
Female N11	11.4	0.5	54.3	5.6	0.3
Female N14	-1.0	-2.1	30.7	0.8	0.2
Female N15	-4.2	2.6	-35.5	-1.2	-0.1
Female N18	11.6	2.7	50.6	5.3	0.1
Female N2	-9.8	-2.7	-59.7	-7.0	-0.2
Female N4	-7.4	-1.6	-58.8	-5.1	-0.4
Male G10	1.9	0.8	143.0	6.7	0.6
Male N11	0.0	-1.9	-8.1	-2.5	0.0
Male N14	8.5	-0.9	3.4	0.7	-0.1
Male N15	-11.7	-1.4	-67.2	-7.8	-0.2
Male N18	12.7	0.7	-8.8	5.0	-0.1
Male N2	-1.4	3.1	-1.9	3.0	0.0
Male N4	-5.1	-0.2	-6.7	-1.3	0.0

PH, plant height; LPP, leaves per plant; LA, leaf area: PC, plant canopy width; STG, stem girth

Table 7. General combining ability effects for traits measured at eight weeks after planting

GCA Effects	PH	LPP	LA	PC	STG	FPI	FPP	HI
Female G10	-22.4	-8.7	109.39	14.4	0.35	-4.68	-126.70	-3.3
Female N11	10.3	-5.4 7	2.63	1.5	0.27	0.72	26.60	-0.3
Female N14	9.9	3.6	11.78	2.8	0.38	-0.14	-52.90	-1.5
Female N15	-4.0	6.4	-58.30	-2.1	-0.20	0.46	54.70	-2.9
Female N18	10.8	8.8	10.65	0.8	0.00	0.88	22.30	2.3
Female N2	-14.2	-5.6	-37.90	-2.6	-0.17	0.43	-9.00	0.2
Female N4	-7.9	-6.3	-26.04	-3.0	-0.01	-1.50	-48.00	2.0
Male G10	-9.0	-0.5	108.13	3.6	0.17	-1.59	-86.10	2.0
Male N11	10.4	-8.0	32.44	-0.6	0.21	1.80	51.70	-4.0
Male N14	4.2	-5.1	24.94	-0.8	0.04	0.50	-24.60	5.9
Male N15	-15.1	7.7	-60.82	-3.2	-0.29	-0.27	-29.30	1.4
Male N18	14.1	0.2	-9.56	1.5	0.04	-0.38	-38.40	-4.1
Male N2	-1.3	4.9	-29.93	0.5	0.03	0.02	71.90	-3.9
Male N4	0.8	-2.6	-20.42	0.7	0.17	-0.78	11.90	1.2

Broad sense and Narrow sense heritability. At 6 WAP, each of the traits had broad sense heritability above 80%. Plant height had the highest broad sense heritability of 99% (Table 8) while stem girth had the lowest at 95%. Narrow sense heritability was highest for leaves per plant and leaf area at 49% and 44% respectively, while lowest narrow sense heritability was observed stem girth at 2%. At 6 WAP, highest baker's ratio was observed in leaves per plant (0.51) followed by leaf area (0.46).

At 8 WAP, all traits exhibited broad sense heritability above 80%. The highest broad sense heritability was 97% observed in leaves per plant while the lowest broad sense heritability was observed in harvest index at 83% (Table 8). Highest narrow sense heritability was exhibited in leaf area (65%) and the lowest narrow sense heritability exhibited in floral traits (0%). At 8 WAP, the highest baker's ratio was observed in leaves per plant (0.66). All the other traits had a baker's ratio less than 0.3. It was also observed that at both 6 and 8 WAP, dominance variance was higher than additive variance for all traits except for leaves per plant at 6 WAP and leaf area at 8 WAP where the additive variance was higher than the dominance variance (Table 8).

Exhibition of high Broad-sense heritability (H2) values indicates that most of the variation observed is genetically determined and that selection among varieties or hybrids will be efficient (Acquaah, 2012). It is possible that the fact that the parents included in the crossing study contained a wide diversity for the traits evaluated also contributed to high H^2 values. When considering narrow-sense heritability (h^2), which takes into account additive variance, values were lower, especially for traits with GCA variance lower than SCA; supporting the conclusion that non-additive gene action is at play in inheritance of these traits. Moreover, Bakers ratio for these traits was low. This therefore means that genes controlling these traits cannot be fixed by the breeder. On the contrary, leaf area and stem girth trait generally had high values for h^2, suggesting a high selection efficiency in breeding.

Table 8. Heritability estimates of the traits measured at six and eight weeks after planting

Trait	Heritability estimate	6 WAP	8 WAP
PH	Additive Variance	296.9	146.8
	Dominance Variance	591.6	1964.4
	Environmental Variance	8.2	77.2
	Phenotypic variance	896.7	2188.4
	H^2	0.99	0.96
	h^2	0.33	0.07
	Baker's ratio	0.33	0.07
PC	Additive Variance	92.64	9.04
	Dominance Variance	214.56	123.24
	Environmental Variance	11.61	8.90
	Phenotypic variance	318.8	141.20
	H^2	0.96	0.94
	h^2	0.29	0.06
	Baker's ratio	0.30	0.07
LPP	Additive Variance	25.36	55.56

	Dominance Variance	24.24	712.72
	Environmental Variance	2.33	22.4
	Phenotypic variance	51.9	790.7
	H^2	0.96	0.97
	h^2	0.49	0.07
	Baker's ratio	0.51	0.07
LA	Additive Variance	13692	13616
	Dominance Variance	15908	6992
	Environmental Variance	1198.67	806.3
	Phenotypic variance	30798.7	21414.3
	H^2	0.96	0.96
	h^2	0.44	0.64
	Baker's ratio	0.46	0.66
STG	Additive Variance	0.168	0.168
	Dominance Variance	0.56	0.40
	Environmental Variance	0.04	0.063
	Phenotypic variance	0.8	0.60
	H^2	0.95	0.90
	h^2	0.22	0.27
	Baker's ratio	0.23	0.30
FPI	Additive Variance		0.00
	Dominance Variance		40.85
	Environmental Variance		1.60
	Phenotypic variance		42.50
	H^2		0.96
	h^2		0.00
	Baker's ratio		0
FPP	Additive Variance		0
	Dominance Variance		58876
	Environmental Variance		2582
	Phenotypic variance		61458
	H^2		0.96
	h^2		0
	Baker's ratio		0
HI	Additive Variance		20.4
	Dominance Variance		64.56
	Environmental Variance		17.72
	Phenotypic variance		102.68
	H^2		0.83
	h^2		0.2
	Baker's ratio		0.23

PH, plant height; LPP, leaves per plant; LA, leaf area: PC, plant canopy width; STG, stem girth; FPI, flowers per inflorescence; FPP, flowers per plant; EY, economic yield; BY, biological yield; HI, harvest index.

Conclusion

The results showed that as a consequence of higher magnitude of interactions, the non-fixable gene effects were higher than the fixable. Therefore, methods which exploit non-additive gene effect such as restricted recurrent selection by the way of inter-mating among desirable segregates, followed by selection or diallel selective mating or multiple crosses or bi-parental mating in early segregating generations could be promising for improvement of this crop.

Acknowledgements

References

Acquaah, G. 2012. Principles of Plant Genetics and Breeding. 2nd Edition, Bowie State University, Maryland USA, ISBN 978-0-470-66476-6 (cloth) — ISBN 978-0-470-66475-9 (pbk.) 1

Adeniji, O.T., Kusolwa, P.M. and Reuben, S.O.W.M. 2012. Genetic diversity among accessions of Solanum aethiopicum L. groups based on morpho-agronomic traits. *Plant Genetic Resources* 10 (3): 177-185.

Bu, S.H., Xinwang, Z., Yi, C., Wen, J., Jinxing, T. and Zhang, Y.M. 2015. Interacted QTL mapping in partial NCII design provides evidences for breeding by design. *PLoS ONE* 10 (3): e0121034. https://doi.org/10.1371/journal.pone.0121034

Covarrubias-Pazaran, G. 2016. Genome assisted prediction of quantitative traits using the R package sommer. *PLoS ONE* 11 (6): p.e0156744.

Daunay, M.C., Aubert, S., Frary, A., Doganlar, S., Lester, R.N., Barendse, G., van der Weerden, G., Hennart, J.W., Haanstra, J., Dauphin, F. and Jullian, E. 2004. Eggplant (*Solanum melongena*) fruit color: pigments, measurements and genetics. pp. 108-116. In: Proceedings of the 12th EUCARPIA Meeting on Genetics and Breeding of Capsicum and Eggplant.

Falconer, D. and Mackay, T.F. 1996. Introduction to Quantitative Genetics, Fourth Edition. Longman, Malaysia.

Fasahat, P., Rajabi .A., Rad, J,M. and Derera, J. 2016. Principles and utilization of combining ability in plant breeding. *Biom Biostat Int J.* 4 (1):1-22. doi: 10.15406/bbij.2016.04.00085..

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences* 9 (4): 463-493.

Hussain K., Hussain, K., Khan, S., Parveen, K., Mukhdoomi, M. I., Nazir, G., Afroza, B., Singh, P. and Dar, Z. 2017. Combining ability analysis in Brinjal (*Solanum melongena* L.). *International Journal of Current Microbiology and Applied Sciences* 6 (7):1645-1655. doi:10.20546/ijcmas.2017.607.199

Jagwe, J., Kasozi, M. and Luwandagga, D. 2016. Demand and supply of African indigenous vegetables (*Solanaceae* sp) in East and Central Uganda. 1–23. https://afri-sol.org/publication/view/final_report_ddss_survey_aivs_25oct2016-002-jj.

Kang, M.S. 2002. Quantitative genetics, genomics, and plant breeding. CABI Pub, Oxon, UK; New York

Kumar, R., Srivastava, K., Singh, N.P., Vasistha, N.K., Singh, R.K. and Singh, M.K. 2013. Combining ability analysis for yield and quality traits in tomato *(Solanum lycopersicum* L.). *Journal of Agricultural Scienc*e 5 (2): 213-218.

Kumar, A., Sharma, V., Jain, B. T. and Kaushik, P. 2020. Heterosis breeding in eggplant (*Solanum melongena* L.): Gains and Provocations. *Plants* 9 (3): 1-16. https://doi.org/10.3390/plants9030403

Lester, R.N. and Seck, A. 2004. *Solanum aethiopicum* L. pp. 530-536. In: Grubben, G.J.H. and O.A. Denton (Eds.), PROTA 2: Vegetables/Légumes. Wageningen, The Netherlands: PROTA

Lewis D. and Jones D.A. 1992. The genetics of heterostyly. pp. 129-150. In: Barrett, S.C.H. (Ed.), Evolution and function of Heterostyly. Monographs on Theoretical and Applied Genetics, Vol 15. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-86656-2_5

Lin, G.R., Li, B.J. and Wei, Y.T. 2006. Inheritance of the white-flower and its influence to related characters in eggplant (*Solanum melongena* Linn). *Yi Chuan* 28 (6):713-6. PMID: 16818435.

Nakyewa, B., Sseremba, G., Kabod, N.P., Rwothtimutung, M., Kyebalyenda, T., Waholi, K., Buteme, R., Nakanwangi, M.J., Bishop, G. and Kizito, E.B. 2021. Farmer preferred traits and genotype choices in *Solanum a ethiopicum* L., Shum group. *Journal of ethnobiology and Ethnomedicine* 17 (1): 1-9.

Nanyanzi, M., Kizito, E., Masanza, M., Sseruwu, G. and Tenywa, M. 2018. Effect of different rates of poultry manure and bio-slurry on the yield of *Solanum aethiopicum* Shum. *Journal of Agricultural Science* 10 (4): 158-166. 10.5539/jas.v10n4p158.

Onyegbule, U.N, Uwanaka,C.E. and Nwosu, P.U. 2018. Growth and fruit yield of graden egg (*Solanum gilo*) as affected by different organic fertilizer types and rates. *Continental J. Agricultural Science* 12 (1): 20-30. doi:10.5281/zenodo.1336619

Pandiyan, M., Savitha, B.K., Veeramani, A., Gopikrishnan, A., Sivakumar, C., Krishnaveni, A., and Radhakrishnan, V. 2020. Studies on inheritance pattern of non spiny character in Spiny Brinjal. *Annals of Agricultural and Crop Sciences* 5 (2): 1-4 .

Pincus, L.M. 2015. Increasing indigenous vegetable yield and nutritional quality through traditionally-and scientifically-informed soil fertility management. University of California, Davis.

Reddy, V. and Varalakshmi, B. 1998. Heterosis and combining ability for leaf yield and its components in vegetable amaranth (*Amaranthus tricolor*). *Indian Journal of Agricultural Sciences* 68: 773-775.

Sprague, G.F. and Tatum, L.A. 1942. General vs. specific combining ability in single crosses of corn. *Journal of the American Society of Agronomy* 34 (10): 923-932.

Sseremba, G., P. T. 2018. Stability of *Solanum aethiopicum* Shum accessions under varied water deficit stress levels and identification of pertinent breeding traits for resistance to water shortage. *Euphytica* 214 (1): 1-11. doi:10.1007/s10681-017-2097-8

Sseremba, G. 2019. Genetic diversity and breeding of *Solanum aethiopicum* Shum group for drought tolerance. PhD Thesis, University of Ghana.

Sseremba, G., Kabod, P., Kasharu, A., Jaggwe, J., Masanza, M., Kizito, E. 2017. Diversity and distribution of African indigenous vegetable species in Uganda. *International Journal of Biodiversity and Conservation* 9 (11): 334-341. 10.5897/IJBC2017.1120.

Thakur P.C. and Verma, T.S. 2000. Combining ability for yield and its components in spinach (*Spinacia aleracea* L.). *Indian Journal of Horticulture* 57 (4): 0972-8538.