

Estimation of gene action in the inheritance of earliness to flowering, sex expression and fruit yield in hybridized native and elite cucumber

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ABSTRACT: Reciprocal crosses between a native cucumber (*Cucumis sativus* L.) variety (*Odukpani*) and 5 elite varieties (*Griffaton*, *Poinsett*, *Ashley*, *Marketmore* and *Monarch*) were carried out in the greenhouse of the Agricultural Services and Training Centre (ASTC), Jos, Plateau State. The F₁ progenies were selfed to obtain the F₂. Backcrosses of F₁ to the seed parent (BC₁) and pollen parent (BC₂) were done to produce the backcross generations. The parents, F₁, F₂, and BC populations were evaluated in the field using RCBD with three replications. Generation means were used to estimate gene action for days to flowering, number of flowers plant⁻¹ and fruit yield. Result of the experiments showed that the additive gene effects were more relevant in the inheritance of days to flowering, number of fruits plant⁻¹ and fresh fruit yield. The effects of digenic interactions, coupled with the significant additive gene effects on flowering and fruit traits for most of the crosses suggest that improvement of these traits could be achieved through breeding methods such as reciprocal recurrent selection which encourages the concentration of genes involved in the inheritance of traits. The contributions of dominance gene effects to the total genetic variance were significant for number of pistillate flowers. This would tend to favour hybridization and the use of first generation hybrids as an effective means of improving female flower production in cucumber. Hence, reciprocal recurrent selection and the use of hybrid programmes are the breeding strategies suggested for enhancing early flowering, gynoecious sex expression and fruit yield in cucumber.

Keywords: Cucumber, elite varieties, gene action, native variety, sex expression.

INTRODUCTION

Cucumber (*Cucumis sativus* L.) belongs to the family *Cucurbitaceae* which comprises about 120 genera and 960 species. It includes many other economically important crops such as melon (*Cucumis melo*), watermelon (*Citrullus lanatus*), and zucchini (*Cucurbita pepo*), which share homologous gene pathways that control similar phenotypes (Bhowmick and Jha, 2015; Li et al., 2019). It is the third most widely grown vegetable crop

and has been used as a model for many genetic studies (Lu et al., 2012). Though cucumber is one of the most popular vegetable species in the *Cucurbitaceae* family, previous studies have reported a low genetic diversity; and detailed insights into the crop's genetic structure and diversity are largely inadequate (Sun et al., 2006). Huang et al. (2009) reported that despite the agricultural and biological importance of cucumber, knowledge of its genetics is very limited and improvement for yield has not been effective since production per unit area has not increased. With current emphasis on consumption of fruits and vegetables to promote good health and life longevity, it is expected that consumption of cucumber should be increased in Nigeria (Eneobong, 2001) and this increase

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must be matched with an increase in cucumber production.

Estimation of genetic parameters is needed to understand the genetic architecture of yield and yield contributing components. Information about the type of gene action would be of immense help to decide on the suitable breeding procedure to be adopted and the characters on which the selection has to be made (Hayman, 1958; Rai et al., 2018). Generation mean analysis is a useful biometric tool that provides the estimation of main genetic effects involved in the expression of traits. It helps to estimate and partition total genetic variance into mean (m), additive (a), dominance (d), additive \times additive (aa), additive \times dominance (ad) and dominant \times dominant (dd) interactions. This technique also provides information about presence or absence of epistasis (Chauhan et al., 2019).

The use of any breeding methods depends on the relative importance of additive and non-additive gene effects. When the former is the main component, progress is achieved with the pedigree selection, whereas the dominance and epistatic gene effects would suggest the use of any breeding methods such as hybridization and reciprocal recurrent selection (Uguru and Ebuka, 1998). Earlier reports in cucumber have implicated additive gene effects in three crosses for sex expression, average fruit weight, fruit girth and fruit yield per hectare (Rai et al., 2018). This information is important but rather inadequate, as the relative importance of both epistatic and non-epistatic gene effects for important agronomic traits such as earliness to flowering, sex expression and fruit yield is useful for deciding the appropriate breeding method to be adopted in cucumber breeding. Additionally, gene action can vary from one population to another in the same crop and estimates of gene effects is essential for a given genetic stock before employing any breeding method for crop improvement (Rai et al., 2018). This study was therefore, carried out to determine the type of gene action in the inheritance of some agronomic characters in crosses between native and elite cucumber varieties with a view to providing effective breeding guide to cucumber breeders.

MATERIALS AND METHODS

The materials for the research comprised five elite cucumber varieties and one indigenous variety from Odukpani in Cross River State, Nigeria. The elite varieties comprised *Griffaton*, *Poinsett*, *Ashley*, *Marketmore* and *Monarch* obtained from seed dealer in Jos, Plateau State, Nigeria. The passport data of the native and elite cucumber varieties used for the research is shown in Table 1.

Reciprocal crosses between the native and elite parental lines were carried out in the greenhouse of the Agricultural Services and Training Centre (ASTC), Jos, Plateau State.

The growth medium for the seedlings in the nursery was a substrate made up of peat, vermiculite and sand mixed at a 1:1:1/2 ratio. Seedlings were raised in seed trays and transplanted from the nursery to the screen house 14 days after planting (DAP). Hybridization of the cucumber varieties was carried out by emasculation and pollinating artificially using a pair of forceps. The forceps was immersed periodically in 70% ethanol between crosses to prevent contamination by unwanted pollens. All the pollinated flowers were carefully tagged. Fruits from successful crosses were allowed to ripe and the seeds processed.

The F₁ progenies were grown in 4 rows of 12 m in the field at the Teaching and Research Farm of College of Agriculture, Garkawa, Plateau State, Nigeria and allowed to self pollinate to obtain the F₂ progenies. In order to prevent cross pollination, the planting dates was staggered at 2 weekly intervals to provide differences in flowering period. The parents and F₁ were raised in the greenhouse and later transplanted to the screen house 14 DAP. Crossing each F₁ to the respective seed parent (BC₁) and pollen parent (BC₂) were done to generate the backcrosses.

The parents, F₁, F₂, and BC populations were evaluated in the field using RCBD with three replications. The plots were weeded manually to keep weed pressure low. Insect pests and diseases were controlled using recommended pesticides and fungicides. Planting was done using intra- and inter- row spacing of 1 m \times 1 m. The plot size was 2 m \times 4 m (8 m²) giving a plant population of 16 per plot at two plants per stand. Weed control was done by manual weeding using small hoe. To achieve optimum fruit yield, NPK 15:15:15 fertilizer was applied at the rate of 120 Kg/ha in two equal split doses at the time of seed sowing and before flowering as recommended by Iwalewa and Amujoyegbe (2019). The data collected comprised days to first flowering (DFF), days to 50% flowering (D50%F), number of staminate flowers plant⁻¹ (NSF/P), number of pistillate flowers plant⁻¹ (NPF/P), number of fruits plant⁻¹ (NFR/P) and fresh fruit yield. Data from the experiments were analyzed using Genstat 10.3 DE statistical package and significant treatment means were separated using the least significant difference (LSD) at 5% level of probability (Obi, 2002).

The means of the parents, F₁, F₂, and BC populations were calculated and the values used to estimate gene action according to Anderson and Kempthome (1954) as modified by Gamble (1962). With some modification of the genetic model of Anderson and Kempthome (1954), Gamble (1962) arrived at six parameters *m*, *a*, *d*, *aa*, *ad* and *dd*. The mean effects *m*, remain the same as K₂; the additive effects, *a* are equal to *F* + *E*; the dominance portion of variation, *d* is equal to 2*E*; the digenic epistatic effects, consisting of the additive \times additive, *aa*, additive \times dominance, *ad*, and dominance \times dominance, *dd*, are equal to *G* + *L* + *M*, 2*G* + *L*, and 4*G*, respectively.

Table 1. Passport data of native and elite cucumber varieties used for the research.

Variety	Source of seed	Description
<i>Odukpani</i>	Odukpani, Cross River State	Unimproved local variety
<i>Griffaton</i>	Jos, Plateau (Imported: Cucumber Breeding Station, *NCSU, USA)	Elite (Exotic)Variety
<i>Poinsett</i>	Jos, Plateau (Imported: Cucumber Breeding Station, NCSU, USA)	Elite (Exotic)Variety
<i>Ashley</i>	Jos, Plateau (Imported: Cucumber Breeding Station, NCSU, USA)	Elite (Exotic)Variety
<i>Marketmore</i>	Jos, Plateau (Imported: Cucumber Breeding Station, NCSU, USA)	Elite (Exotic)Variety
<i>Monarch</i>	Jos, Plateau (Imported: Cucumber Breeding Station, NCSU, USA)	Elite (Exotic)Variety

*NCSU= North Carolina State University

The six populations comprising the parents (P_1 and P_2), F_1 , F_2 , P_1F_1 and P_2F_1 were used in this study to estimate the parameters m , a , d , aa , ad and dd as follows:

$$m = \bar{F}_2$$

$$a = \bar{P}_1\bar{F}_1 - \bar{P}_2\bar{F}_1$$

$$d = -\frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + \bar{P}_1\bar{F}_1 - \bar{P}_2\bar{F}_1$$

$$aa = -4\bar{F}_2 + 2\bar{P}_1\bar{F}_1 - 2\bar{P}_2\bar{F}_1$$

$$ad = -\frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2 + \bar{P}_1\bar{F}_1 - \bar{P}_2\bar{F}_1$$

$$dd = \bar{P}_1 - \bar{P}_2 + 2\bar{F}_1 - 4\bar{F}_2 - 4\bar{P}_1\bar{F}_1 - 4\bar{P}_2\bar{F}_1$$

Where: m = F_2 population mean, a = additive gene effect, d = dominant gene effect, $a \times a$ = additive \times additive type of epistasis, $a \times d$ = additive \times dominance type of epistasis, $\bar{F}_1\bar{P}_1$ = mean of F_1 crossed with P_1 , $\bar{F}_2\bar{P}_2$ = means of F_1 crossed with P_2 , \bar{P}_1 and \bar{P}_2 = means of the two parents, and \bar{F}_1 and \bar{F}_2 = means of the F_1 and F_2 populations, respectively.

Estimates of variances were determined as described by Falconer (1989) and Uguru and Uzo (1991) as exemplified below:

$$\sigma^2_a = \sigma^2 P_1 F_1 - \sigma^2 P_2 F_1$$

$$\sigma^2_d = \frac{1}{4}\sigma^2 P_1 + \frac{1}{4}\sigma^2 P_2 + \sigma^2 F_1 + 16\sigma^2 F_2 + 4\sigma^2 P_1 F_1 + 4\sigma^2 P_2 F_1$$

where: σ^2_a = variance due to additive gene effects and σ^2_d = variance due to dominance gene effects

RESULTS AND DISCUSSION

Generation mean analysis is an important tool to estimate the contributions of additive and non-additive gene effects and the presence or absence of epistasis. The generation means for flowering traits assessed in this study for the F_1 ,

F_2 and backcross (BC_1 and BC_2) populations for crosses between native and elite cucumber showed that values for days to first flowering for the F_1 and F_2 populations differed significantly and ranged from 29.7 to 48.1 days and 30.5 to 42.4 days, respectively (Table 2). The backcrosses recorded mean days to first flowering of 30.0 to 40.5 days (BC_1) and 30.1 to 42.9 days (BC_2). Days to 50% flowering among the progenies ranged from 32.7 to 54.7 days (F_1), 33.0 to 44.3 days (F_2), 31.8 to 50.2 days (BC_1) and 32.7 to 50.3 days (BC_2). Number of staminate flowers varied from 129.9 to 211.0 (F_1), 138.8 to 199.6 (F_2), 131.5 to 221.0 (BC_1) and 170.4 to 192.3 (BC_2); while mean values for pistillate flowers ranged from 39.4 to 46.2, 27.8 to 45.5, 34.3 to 48.3 and 39.0 to 46.8 for the F_1 , F_2 , BC_1 and BC_2 , in that order. Variations in flowering traits for gynoecious cucumber have been reported (Kumar *et al.*, 2017).

Fruit traits for the F_1 , F_2 and backcross populations showed substantial differences for number of fruits and fresh fruit yield (Table 3). Number of fruits plant^{-1} ranged from 12.05 in *Odukpani* x *Monarch* to 15.37 in *Monarch* x *Odukpani* (F_1), 10.53 in *Odukpani* x *Monarch* to 16.61 in *Griffaton* x *Odukpani* (F_2), 12.96 in *Odukpani* x *Monarch* to 15.81 in *Odukpani* x *Griffaton* (BC_1) and 12.01 in *Odukpani* x *Monarch* to 14.91 in *Odukpani* x *Griffaton* (BC_2). The mean values of fresh fruit yield also varied from 12.70 t ha^{-1} (*Monarch* x *Odukpani*) to 17.10 t ha^{-1} (*Odukpani* x *Monarch*), 13.03 t ha^{-1} (*Monarch* x *Odukpani*) to 17.34 t ha^{-1} (*Odukpani* x *Griffaton*), 13.01 t ha^{-1} (*Monarch* x *Odukpani*) to 16.97 t ha^{-1} (*Odukpani* x *Griffaton*) and 12.24 t ha^{-1} (*Odukpani* x *Poinsett*) to 15.87 t ha^{-1} (*Griffaton* x *Odukpani*) for the F_1 , F_2 , BC_1 and BC_2 , respectively (Table 3).

The differences in generation mean values for fruit traits among the progenies and the substantial increase in these traits for progenies, relative to the parents, implied cucumber growers could use early generations as planting materials and be assured of high fruit yield. There is also the possibility of selecting and advancing superior individual plants from the backcrosses, the F_2 and subsequent segregating populations.

Estimates of additive gene effects for days to first and 50% flowering were significant and positive for half of the

Table 2. Generation means for flowering traits for parents, F₁, F₂ and backcross populations of crosses between native and elite cucumber varieties.

Crosses	Days to first flowering						Days to 50% flowering					
	P ₁	F ₁	F ₂	P ₂	BC ₁	BC ₂	P ₁	F ₁	F ₂	P ₂	BC ₁	BC ₂
Odukpani x Griffaton	46.5	48.1	34.5	30.3	36.0	30.8	51.5	52.3	44.3	33.5	46.0	34.5
Odukpani x Poinsett	46.5	46.9	42.4	30.0	35.9	30.1	51.5	51.9	43.9	32.5	47.2	33.0
Odukpani x Ashley	46.5	47.1	35.5	30.5	40.5	30.2	51.5	53.2	44.0	33.0	47.8	32.9
Odukpani x Marketmore	46.5	47.8	39.0	31.5	35.0	31.6	51.5	54.7	42.1	33.5	47.1	33.2
Odukpani x Monarch	46.5	46.7	39.9	31.6	36.0	31.2	51.5	51.7	41.5	34.5	46.9	32.7
Griffaton x Odukpani	30.3	29.7	30.5	46.5	30.3	36.5	33.5	32.7	33.0	51.5	34.0	47.1
Poinsett x Odukpani	30.0	30.7	30.6	46.5	30.0	37.1	32.5	32.9	33.5	51.5	32.9	46.3
Ashley x Odukpani	30.5	31.3	30.9	46.5	31.8	41.7	33.0	33.1	33.6	51.5	31.8	46.6
Marketmore x Odukpani	30.5	31.5	31.5	46.5	31.3	40.2	33.0	34.1	34.0	51.5	32.0	45.8
Monarch x Odukpani	31.5	31.0	31.2	46.5	30.6	42.9	33.5	33.7	33.9	51.5	33.2	46.3
Number of staminate flowers plant ⁻¹						Number of pistillate flowers plant ⁻¹						
Odukpani x Griffaton	128.8	130.4	148.5	169.5	131.5	144.3	25.0	45.7	27.8	43.3	36.5	46.0
Odukpani x Poinsett	128.8	129.9	138.8	165.7	149.9	157.9	25.0	40.2	40.6	39.7	35.0	41.0
Odukpani x Ashley	128.8	172.3	169.0	183.3	172.3	182.0	25.0	43.4	39.6	40.3	34.3	42.1
Odukpani x Marketmore	128.8	181.5	170.4	195.4	171.5	185.1	25.0	46.2	30.8	45.7	37.2	46.8
Odukpani x Monarch	128.8	179.5	160.3	167.3	159.5	162.9	25.0	39.4	44.1	38.4	34.7	39.0
Griffaton x Odukpani	169.5	211.0	174.1	165.7	221.0	170.4	43.3	45.3	45.5	39.7	45.0	40.6
Poinsett x Odukpani	165.7	165.1	178.3	183.3	167.5	159.0	39.7	42.0	41.0	40.3	43.0	40.1
Ashley x Odukpani	183.3	173.6	199.6	195.4	193.6	192.3	40.3	46.0	45.8	45.7	42.5	45.9
Marketmore x Odukpani	183.3	174.0	190.4	167.3	184.0	171.5	40.3	44.3	40.5	38.4	43.6	42.0
Monarch x Odukpani	195.4	161.9	198.7	167.3	171.9	167.5	45.7	46.0	39.0	38.4	48.3	44.8

crosses (Table 4). The preponderance of additive gene action for days to first and 50% flowering obtained for crosses in this study suggests that the additive gene effects made major contributions to the total genetic variations. According to Gamble (1962), the additive gene effects become positive when the better performing inbred parent is used as the pistillate plant.

The additive x additive type of epistasis for days

to first and 50% flowering were significant in most crosses, but values were negative in crosses with the native variety as the maternal parent. The dominance x dominance epistatic effects for days to first and 50% flowering were significant and values were also negative in all the crosses (Table 4). The opposite signs for the estimates of dominance and dominance x dominance gene effects in this study implied that they were of the

duplicate type for days to first flowering and number of pistillate flowers; while it showed the complementary type of gene effects for days to 50% flowering and number of staminate flowers plant⁻¹. Mather and Jinks (1971) reported that when dominance and dominance x dominance gene effects have the same sign, the interaction is of complementary type, but when they have opposite signs, interaction is of the duplicate type.

Table 3. Generation mean of some fruit traits for parents, F_1 , F_2 and backcross populations of crosses between native and elite cucumber varieties.

Crosses	Number of fruits/plant						Fresh fruit yield ($t ha^{-1}$)					
	P_1	F_1	F_2	P_2	BC_1	BC_2	P_1	F_1	F_2	P_2	BC_1	BC_2
<i>Odukpani x Griffaton</i>	11.86	14.90	15.56	15.61	15.81	14.91	11.86	17.10	17.34	16.61	16.97	15.79
<i>Odukpani x Poinsett</i>	11.86	13.03	11.57	11.98	14.27	13.50	11.86	13.87	16.06	11.98	13.98	12.47
<i>Odukpani x Ashley</i>	11.86	13.71	11.81	13.14	14.89	13.19	11.86	14.86	16.49	13.14	15.21	14.32
<i>Odukpani x Marketmore</i>	11.86	13.90	14.09	13.83	14.99	13.56	11.86	14.67	17.12	13.83	14.92	13.76
<i>Odukpani x Monarch</i>	11.86	12.05	10.53	11.66	12.96	12.01	11.86	13.46	15.23	11.66	13.98	12.90
<i>Griffaton x Odukpani</i>	16.61	15.02	16.61	11.86	15.39	14.26	16.61	16.90	16.51	11.86	16.95	15.87
<i>Poinsett x Odukpani</i>	11.98	12.54	11.98	11.86	13.80	12.19	11.98	13.28	16.32	11.86	14.02	13.98
<i>Ashley x Odukpani</i>	13.14	13.32	13.14	11.86	13.85	13.01	13.14	14.18	15.98	11.86	14.34	13.72
<i>Marketmore x Odukpani</i>	13.83	13.82	13.83	11.86	14.02	12.29	13.83	14.67	14.99	11.86	14.89	13.61
<i>Monarch x Odukpani</i>	11.66	15.37	11.66	11.86	15.41	13.37	11.66	12.70	13.03	11.86	13.01	12.24

Table 4. Estimates of gene effects for days to flowering in crosses between native and elite cucumber varieties.

Traits	Cross	<i>m</i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
Days to first flowering	<i>Odukpani X Griffaton</i>	34.5	5.2*	27.05	-4.4	-2.2	-46.4*
	<i>Odukpani X Poinsett</i>	42.4	5.8*	16.7	-37.6*	-2.5*	-82.5*
	<i>Odukpani X Ashley</i>	35.5	10.3*	28.35	-0.6	-0.9	-73.0*
	<i>Odukpani X Marketmore</i>	39.0	3.4*	22.95	-22.8*	-3.7*	-59.0*
	<i>Odukpani X Monarch</i>	39.9	4.8*	18.95	-25.2*	-7.95*	-70.5*
	<i>Griffaton X Odukpani</i>	30.5	-6.2	38.4	11.6*	-1.3	-54.0*
	<i>Poinsett X Odukpani</i>	30.6	-7.1	37.25	11.8*	-3.45*	-49.1*
	<i>Ashley X Odukpani</i>	30.9	-9.9	46.1	23.4*	-0.4	-37.4*
	<i>Marketmore X Odukpani</i>	31.5	-8.9	39.85	17.0*	-3.6*	-43.4*
	<i>Monarch X Odukpani</i>	31.2	-12.3*	44.35	22.2*	38.1*	-28.6*

The dominance gene effects for mean number of pistillate flowers were positive and similar in magnitudes to the F_2 means (Table 5). Additive x additive epistatic effects for number of staminate

and pistillate flowers for crosses between the native and elite cucumber varieties were significant for most crosses. The additive x dominance epistasis were significant and positive in six

crosses (*Odukpani x Poinsett*, *Odukpani x Ashley*, *Odukpani x Marketmore*, *Odukpani x Monarch*, *Griffaton x Odukpani* and *Pinsett x Odukpani*) for number of staminate flowers and in two crosses

Table 4. Contd.

Traits	Cross	<i>m</i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
Days to 50% flowering	<i>Odukpani</i> X <i>Griffaton</i>	44.30	11.5*	-86.90	-16.2*	2.50*	-100.6*
	<i>Odukpani</i> X <i>Poinsett</i>	43.90	14.2*	-85.50	-15.2*	4.70*	-109.6*
	<i>Odukpani</i> X <i>Ashley</i>	44.00	14.9*	-84.35	-14.6*	5.65*	-110.7*
	<i>Odukpani</i> X <i>Marketmore</i>	42.10	13.9*	-75.90	-7.8	4.90*	-96.6*
	<i>Odukpani</i> X <i>Monarch</i>	41.50	14.2*	-77.70	-6.8	5.70*	-102.4*
	<i>Griffaton</i> X <i>Odukpani</i>	33.00	-13.1*	-60.70	30.2*	-4.10*	-32.2*
	<i>Poinsett</i> X <i>Odukpani</i>	33.50	-13.4*	-63.90	24.4*	-3.90*	-33.6*
	<i>Ashley</i> X <i>Odukpani</i>	33.60	-14.8*	-65.15	22.4*	-5.55*	-27.5*
	<i>Marketmore</i> X <i>Odukpani</i>	34.00	-13.8*	-66.35	19.6*	-4.55*	-31.1*
	<i>Monarch</i> X <i>Odukpani</i>	33.90	-13.1*	-64.90	23.4*	-4.10*	-33.8*

m = F_2 mean, *a* = additive gene effects, *d* = dominance gene effects, *aa* = additive x additive epistasis, *ad* = additive x dominance epistasis, *dd* = dominance x dominance epistasis.

Table 5. Estimates of gene effects for number of flowers in crosses between native and elite cucumber varieties.

Traits	Cross	<i>m</i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
Number of staminate flowers	<i>Odukpani</i> X <i>Griffaton</i>	148.5	-12.80	-264.7*	-42.4*	7.5	-322.7*
	<i>Odukpani</i> X <i>Poinsett</i>	138.8	-8.00	-305.5*	60.4*	10.5*	-300.3*
	<i>Odukpani</i> X <i>Ashley</i>	169	-9.70	-305.6*	32.6*	17.6*	-347.1*
	<i>Odukpani</i> X <i>Marketmore</i>	170.4	-13.60	-287.3*	31.6*	19.7*	-330.8*
	<i>Odukpani</i> X <i>Monarch</i>	160.3	-3.40	-261.6*	3.6	15.8*	-307.1*
	<i>Griffaton</i> X <i>Odukpani</i>	174.1	50.60	-396.1*	86.4*	48.7*	-473.0*
	<i>Poinsett</i> X <i>Odukpani</i>	178.3	8.50	-428.2*	-60.2*	17.3*	-434.6*
	<i>Ashley</i> X <i>Odukpani</i>	199.6	1.30	-407.4*	-26.6*	7.4	-468.5*
	<i>Marketmore</i> X <i>Odukpani</i>	190.4	12.50	-474.8*	-50.6*	4.5	-447.6*
	<i>Monarch</i> X <i>Odukpani</i>	198.7	4.40	0.00	-16.0	-9.6	-460.5*
Number of pistillate flowers	<i>Odukpani</i> X <i>Griffaton</i>	27.8	-9.5	49.45*	-53.8*	-0.35	-0.1
	<i>Odukpani</i> X <i>Poinsett</i>	40.6	-6.0	57.95*	-10.4*	1.35*	-72.7*
	<i>Odukpani</i> X <i>Ashley</i>	39.6	-7.8	50.95*	-5.6	-0.15	-55.7*
	<i>Odukpani</i> X <i>Marketmore</i>	30.8	-9.6	52.45*	-44.8*	-0.75*	-13.1*
	<i>Odukpani</i> X <i>Monarch</i>	44.1	-4.3	55.9*	-29.0*	2.4	-93.8*
	<i>Griffaton</i> X <i>Odukpani</i>	45.5	4.4*	19.7*	10.8*	2.6	-105.4*
	<i>Poinsett</i> X <i>Odukpani</i>	41.0	2.9	22.3*	2.2	3.2*	-92.2*
	<i>Ashley</i> X <i>Odukpani</i>	45.8	3.4*	20.2*	6.4	-0.7	-83.0*
	<i>Marketmore</i> X <i>Odukpani</i>	40.5	1.6	24.65*	9.2*	-0.65*	-77.9*
	<i>Monarch</i> X <i>Odukpani</i>	39.0	3.5*	21.15*	30.2*	-0.15	-70.7*

m = F_2 mean, *a* = additive gene effects, *d* = dominance gene effects, *aa* = additive x additive epistasis, *ad* = additive x dominance epistasis, *dd* = dominance x dominance epistasis.

(*Griffaton* x *Poinsett* and *Poinsett* x *Odukpani*) for number of pistillate flowers plant⁻¹. The positive dominance gene effects in all the crosses for number of pistillate flowers implicated the dominance gene component as the principal contributor to the variations for this trait. This

report is in agreement with the dominance gene action reported by Kumar et al. (2017) in cucumber, Tassawar et al. (2007) in corn and Uguru and Ebuka (1998) in castor. Conversely, Rai et al. (2018) reported significant additive gene effect in three crosses for sex expression.

Table 6. Estimates of gene effects for number of fruits and fresh fruit yield in crosses between native and elite cucumber varieties.

Traits	Cross	<i>m</i>	<i>a</i>	<i>d</i>	<i>aa</i>	<i>ad</i>	<i>dd</i>
Number of fruits plant ⁻¹	<i>Odukpani</i> X <i>Griffaton</i>	15.5	-0.1	-60.2*	-2.6	2.6*	-37.2*
	<i>Odukpani</i> X <i>Poinsett</i>	11.5	-0.3	-44.6	7.4*	0.7	-20.8*
	<i>Odukpani</i> X <i>Ashley</i>	11.8	0.0	-45.0	8.4*	1.2*	-22.2*
	<i>Odukpani</i> X <i>Marketmore</i>	14.0	0.1*	-54.4*	0.2	2.2*	-32.7*
	<i>Odukpani</i> X <i>Monarch</i>	10.5	0.8*	-40.3	8.0*	1.6*	-22.8*
	<i>Griffaton</i> X <i>Odukpani</i>	15.6	2.7*	-58.7*	-4.2	1.0	-39.8*
	<i>Poinsett</i> X <i>Odukpani</i>	12.5	0.1	-49.9*	1.8	0.3	-25.8*
	<i>Ashley</i> X <i>Odukpani</i>	14.3	-1.1	-58.6*	-1.0	-0.3	-27.9*
	<i>Marketmore</i> X <i>Odukpani</i>	12.5	1.1*	-47.4*	3.8	0.7	-26.0*
	<i>Monarch</i> X <i>Odukpani</i>	12.0	1.7*	-44.5	10.2*	0.45	-22.3*
Fresh fruit yield (t ha ⁻¹)	<i>Odukpani</i> X <i>Griffaton</i>	17.34	1.2*	-33.7*	-3.8*	3.6*	-44.6*
	<i>Odukpani</i> X <i>Poinsett</i>	16.06	1.5*	-35.8*	-11.3*	1.6*	-42.7*
	<i>Odukpani</i> X <i>Ashley</i>	16.49	0.9*	-34.1*	-6.9*	1.5*	-41.1*
	<i>Odukpani</i> X <i>Marketmore</i>	17.12	1.2*	-37.9*	-11.1*	2.2*	-45.8*
	<i>Odukpani</i> X <i>Monarch</i>	15.23	1.1*	-32.3*	-7.2*	0.9*	-38.2*
	<i>Griffaton</i> X <i>Odukpani</i>	16.51	1.1*	-30.6*	-0.40	-1.30	-31.8*
	<i>Poinsett</i> X <i>Odukpani</i>	16.32	0.1	-35.9*	-9.3*	-0.02	-38.8*
	<i>Ashley</i> X <i>Odukpani</i>	15.98	0.6*	-34.2*	-7.8*	-0.02	-36.7*
	<i>Marketmore</i> X <i>Odukpani</i>	14.99	1.3*	-29.6*	-2.9	0.30	-33.8*
	<i>Monarch</i> X <i>Odukpani</i>	13.03	0.8*	-25.9*	-1.6	0.8*	-30.0*

m = F₂ mean, *a* = additive gene effects, *d* = dominance gene effects, *aa* = additive x additive epistasis, *ad* = additive x dominance epistasis, *dd* = dominance x dominance epistasis.

Estimates of the additive gene effects for number of fruits plant⁻¹ and fresh fruit yield were significant and positive in most crosses, while dominance gene effects recorded negative values for all crosses for these traits (Table 6). The additive x additive epistases for number of fruits plant⁻¹ were significant for four crosses. The additive x dominance type of epistasis were significant and positive in four and six crosses for number of fruits plant⁻¹ and fresh fruit yield, respectively. The estimates of epistatic gene effects: additive x additive, additive x dominance and dominance x dominance in some of the crosses were high enough to be potentially important (Hayman, 1958). The dominance x dominance epistasis was significant in most crosses and its values were essentially negative. This is expected because of the high heterotic value associated with the F₁ progenies, since dominance x dominance gene effects do not contribute to heterotic performance (Gamble, 1962). The additive gene effects were more relevant in determining number of fruits plant⁻¹ and fresh fruit yield. Rai *et al.* (2018) reported similar additive gene effects for a cross (ACS12-31 x B19) with duplicate epistasis and recommended recurrent selection method for the improvement of the crop. The dominance gene effects were negative and of the complimentary type implying minimal contributions of the dominance

component for gene action.

The additive gene effects implied that the improvement of traits can be enhanced with any breeding method that would encourage the concentration of genes for days to flowering, number of fruits plant⁻¹ and fresh fruit weight. The reciprocal recurrent selection is recommended as a breeding method for improving these traits. The significant dominance gene effects for number of pistillate flowers showed that female flower production in cucumber could be improved by hybridization. Hence, the reciprocal recurrent selection and the use of hybrid programmes are the breeding strategies suggested for enhancing early flowering, gynoecious sex expression and fruit yield in cucumber.

Conclusion

The variations in generation mean values for days to flowering, number of flowers and fruit traits among the progenies and the substantial increase in these traits for progenies, relative to the parents, implied cucumber growers could use these early generations as planting materials and be assured of early harvest and high fruit yield. The additive gene effects for days to flowering and

fruit yield suggests that reciprocal recurrent selection is recommended as a breeding method for improving these traits. The dominance gene effects for number of pistillate flowers implied that female flower production in cucumber could be improved by hybridization. Thus, the reciprocal recurrent selection and the use of hybrid programs are the breeding strategies suggested for enhancing early flowering, gynoecious sex expression and fruit yield in cucumber.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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