Hybrid vigour and gene action for two quantitative traits of castor plant (*Ricinus communis* L.)

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SUMMARY

Five homozygous lines of castor plant, namely RS_1-O_m, RN_1-O_m, RT_1-2_m, RS_1-O_{wm}, and RN_1-O_{mb}, were crossed to raise F_1, F_2, BC_1, and BC_2 generations. The hybrids were tested for hybrid vigour for two metric traits, *viz*; number of pods per plant and seed yield per plant. Highly significant hybrid vigour was detected for both traits in all the crosses. The contributions of additive and non-additive gene effects to both traits were also investigated. Additive gene effects were more relevant in the inheritance of number of pods per plant. The effects of the digenic interactions, coupled with the highly significant additive gene effects on number of pods per plant in most of the crosses, tend to suggest that improvement of the character can be enhanced by the use of breeding methods such as the reciprocal recurrent selection that would encourage the concentration of genes involved in the inheritance of the trait. The contributions of dominance gene effects to the total genetic variance were positive and highly significant in both pod and seed yield per plant in all the hybrids. This would tend to favour hybridization and the use of first generation hybrids as an effective means of improving both traits in castor plant. Thus, reciprocal recurrent selection and the use of hybrid programmes are the breeding strategies suggested for the improvement of pod and seed yield in castor plant.

RÉSUMÉ

UGURU, M. I. & ABUKA, L. N.: *La vigueur hybride et l'action de gène pour deux traits quantitatives de ricin (Ricinus communis L.).* Cinq lignes homozygotes de ricin, à savoir, $RS_1- O_m$, $RN_1- O_m$, RT_1-2_m, $RS_1- O_{wm}$ et $RN_1- O_{mb}$, étaient croisées pour élever les générations de F_1, F_2, BC_1 et BC_2. Les hybrides étaient essayés pour la vigueur hybride pour duex traits métriques c'est-à-dire, nombre des cosses par plante et le rendement de graine par plante, La vigueur hybride hautement considérable était détectée pour les deux traits dans tous les croisements. Les contributions des effets de gène additif et non additif aux deux traits étaient également enquêtées. Les effets de gène additif étaient plus utiles dans l'héritage de nombre des cosses par plante. La nature des effets d'interactions digéniques ajoutés aux effets de gène additif hautement considérable sur nombre des cosses par plante dans la plupart de croisements ont la tendance à suggérer que l'amélioration du caractère peut être augmentée par l'emploi de méthode de reproduction telle que la sélection récurrente réciproque que pourrait encourager la concentration de gène entraînés dans l' héritage du trait. Les contributions des effets de gène dominant à la variance génétique totale étaient positives et hautement considérables dans le rendement de cosse et de graine à la fois par plante en tous les hybrides. Ceci pourraite avoir la tendance à favoriser la hybridation et l'emploi des hybrides de la première génération comme un moyen efficace d' améliorer les deux traits de ricin. Ainsi, la sélection récurrente réciproque et l' usage des programmes hybrides sont les stratégies de reproduction sugérées pour l'amélioration du rendement de cosse et de graine en ricin.

Introduction

Castor plant (*Ricinus communis* L.), as compared to other crops with known industrial potentials, has attracted little and fragmentary research efforts, particularly in tropical West Africa where organized planting is rare and harvests are made mainly from volunteer crops. As a result, the yield has been generally low and largely unreliable.

In Nigeria, selection is based on the farmer's discretion in that seeds of impressive castor plants

are simply kept for the next season's planting. Several local cultivars, varying greatly in both growth and yield characters, have arisen from this selection process. As a means of increasing and ensuring a reasonably high yield, the locally available cultivars need to be improved through the development and supply of single cross hybrid seeds. This will enable castor plant growers to exploit hybrid vigour as has been done in maize (Krolikowski, 1969), sesame (Chaudhari *et al.,* 1979), sunflower (Sudhakaz, 1979), rye (Kobyljanskij & Kosov, 1971), millet (Singh & Lal, 1969), sorghum (Sepel, 1968), cowpea (De Mooy, 1985), and guar (Mithal & Thomas, 1969). Other effective breeding methods include reciprocal and non-reciprocal recurrent selections.

The use of any of these methods is, however, determined by the relative importance of the additive and non-additive gene effects. When the former is the main component, progress is maximum with the pedigree selection (El- Agamy, Eweida & Okaz, 1975), whereas the dominance and epistatic gene effects would suggest the use of breeding methods such as hybridization and reciprocal recurrent selection. Earlier reports have implicated the dominance gene effects for some pods in castor plant (Narkhede *et al.,* 1987). This information is important but rather inconclusive, as the relative importance of both epistatic and non-epistatic gene effects in each of the traits is useful in deciding the best breeding procedure to be adopted.

The study aimed to design experiments to investigate whether crosses between castor plants contrasting in many respects would show useful F_1 hybrid vigour, and also contribute information for the study of gene action in two metric traits, namely number of pods per plant and seed yield per plant. The latter objective would aid in the choice of an effective breeding method and accelerate improvement of castor plant.

Materials and methods

The materials for the study comprised five castor genotypes, namely RS_1-O_m, RN_1-O_m, RT_1-2_m, RS_1- O_{wm}, and RN_1-O_{mb}, collected from the Department of Crop Science, University of Nigeria, Nsukka, Nigeria, as inbreds generated by self-fertilization.

Four crosses were made among the genotypes as follows:

(i) RS_1-O_m × RN_1-O_m
(ii) RS_1-O_m × RN_1-2_m
(iii) RS_1-O_{wm} × RN_1-O_{mb}
(iv) RS_1-O_{mb} × RN_1-O_m

Backcrosses of the hybrids (i), (ii), (iii), and (iv) to their respective parents were made to produce the BC_1 and BC_2 generations, respectively. The F_2 seeds were produced by natural self pollination of the F_1 generation.

The parents, F_1, F_2, BC_1 (P_1 × F_1) and BC_2 (P_2 × F_1) were evaluated in randomized complete block design (RCBD) with three replications. Single-row plots of 8 m² each were used for the evaluations. Each row consisted of four plants, and measurements were taken on the two plants in the middle of each row. Pods per plant were counted and seed yield per plant was determined by measuring the weight of all the seeds harvested from the sampled plants after drying. Plot means were computed and expressed as means of single plants. Means across replications were used for calculating heterosis and over-dominance according to Sotomayor-Rios & Torres Cardona (1984). The student t-test at 5 per cent probability level was used to determine significant heterosis and over-dominance.

The means of the parents, F_1, F_2, BC_1, and BC_2 generations, were calculated and the values were used to estimate gene action according to Anderson & Kempthorne (1954) as modified by Gamble (1962). Anderson & Kempthorne's model uses the means of populations resulting from crossing two homozygous lines followed by subsequent crossing and selfing. By applying the factorial model to the populations arising from the cross between the two parents and the descendants of crossing and selfing, they derived six parameters, *viz:* K_2 representing the mean effects; E and F representing non-epistatic effects; and G, L, and M representing epistatic effects.

Trigenic and higher interactions were assumed negligible. With some modifications of the genetic model of Anderson & Kempthorne (1954), Gamble (1962) arrived at the six parameters m, a, d, aa, ad and dd. The mean effects m, remain the same as K_2; the additive effects, a are equal to $F + E$; the dominance portion of variation, d is equal to $2E$; the digenic epistatic effects, consisting of the additive × additive, aa, additive × dominance, ad, and dominance × dominance, dd are equal to $G + L + M$, $2G + L$, and $4G$, respectively, in the Anderson & Kempthorne model.

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:

$$m = F_2$$
$$a = P_1F_1 - P_2F_1$$
$$d = -\tfrac{1}{2}P_1 - \tfrac{1}{2}P_2 + F_1 - 4F_2 + P_1F_1 + P_2F_1$$
$$aa = -4F_2 + 2P_1F_1 + 2P_2F_1$$
$$ad = -\tfrac{1}{2}P_1 + \tfrac{1}{2}P_2 + P_1F_1 - P_2F_1$$
$$dd = P_1 - P_2 + 2F_1 - 4F_2 - 4P_1F_1 - 4P_2F_1$$

where

m = F_2 population mean
a = additive gene effect
d = dominance gene effect
$a \times a$ = additive × additive type of epistasis
$a \times d$ = additive × dominance type of epistasis

P_1F_1 = mean of F_1 crossed to P_1
P_2F_2 = mean of F_1 crossed to P_2
P_1 and P_2 = means of the two parents
F_1 and F_2 = means of the F_1 and F_2 populations, respectively.

The variances of the estimates were determined according to Falconer (1989) and Uguru & Uzo (1991) as exemplified below:

$$\sigma_a^2 = \sigma^2 P_1F_1 - \sigma^2 P_2F_1$$
$$\sigma_d^2 = \tfrac{1}{4}\sigma^2 P_1 + \tfrac{1}{4}\sigma^2 P_2 + \sigma^2 F_1 + 16\sigma^2 F_2 + 4\sigma^2 P_1F_1 + 4\sigma^2 P_2F_1$$

where

σ_a^2 = variance due to additive gene effects
σ_d^2 = variance due to dominance gene effects

To test for significance, the 't' test was used as the test statistic based on El-Agamy et al. (1975).

$$\pm t = \frac{\text{effect}}{\sqrt{\text{variance of effect}}}$$

Results

Table 1 shows the data on generation means of the parents, F_1, F_2, BC_1 and BC_2 for the traits. Table 2 shows the heterotic and over-dominance values and Table 3 shows the type of gene effects derived from the generation means.

TABLE 1

Generation Means of Parents, F_1, F_2, BC_1 and BC_2 in Four Crosses Based on Pods per Plant and Seed Yield per Plant

Character	Cross	P_1	F_1	F_2	P_2	BC_1	BC_2
Number of pods per plant	(i)*	342	499	289	203	516	278
	(ii)	342	502	294	93	361	202
	(iii)	168	369	233	137	549	416
	(iv)	137	371	231	203	246	503
Seed yield per plant	(i)	143.7	213.5	112.7	95.0	282.5	135.5
	(ii)	143.7	402.4	223.6	156.4	215.0	315.1
	(iii)	184.5	209.7	171.9	129.1	206.9	254.6
	(iv)	129.1	194.1	126.1	95.0	149.8	322.9

(i)+ = $RS_1 - 0_m \times RN_1 - 0_m$
(ii) = $RS_1 - 0_m \times RT_1 - 2_m$
(iii) = $RS_1 - 0_{wn} \times RN_1 - 0_{mb}$
(iv) = $RN_1 - 0_{mb} \times RN_1 - 0_m$

Percentage Increase Over Mid-parent (Heterosis) and Over Better Parent (Over-dominance) in Number of Pods per Plant and Seed Yield per Plant

	Pods per plant		Seed yield per plant	
Cross	Heterosis	Over-dominance	Heterosis	Over-dominance
(i)+	0.83**	0.46**	0.79**	0.49**
(ii)	1.30**	0.47**	1.68**	1.57**
(iii)	1.41**	1.20**	0.34**	0.14**
(iv)	1.18**	0.83**	0.73**	0.50**

** Significant at 1 per cent probability level.

(i)+ = $RS_1 - O_m \times RN_1 - O_m$
(ii) = $RS_1 - O_m \times RT_1 - 2_m$
(iii) = $RS_1 - O_{wm} \times RN_1 - O_{mb}$
(iv) = $RN_1 - O_{mb} \times RN_1 - O_m$

and highly significant in crosses (i), (ii) and (iii) but negative in cross (iv) (Table 3). Dominance gene effect was positive and highly significant in all the crosses. Additive × additive gene effect followed a similar trend except in the cross RS_1-$O_m \times RT_1$-2_m where the value was negative and non-significant. Additive × dominance epistasis was only significant in the crosses RS_1-$O_m \times RN_1$-O_m and RN_1-$O_{mb} \times RN_1$-O_m. Although dominance × dominance gene effects were highly significant in all the crosses, the effect was only positive in the cross RS_1-$O_m \times RT_1$-2_m.

Seed yield per plant
    Highly significant heterosis over the mid-parent

Estimates of the Six Gene Effects for the Four Crosses Based on Number of Pods and Seed Yield per Plant

Character	Cross	m	a	d	aa	ad	dd
Pods per plant	(i)+	289**	238**	667.5**	432*	473**	-477.0**
	(ii)	294**	159**	234.5**	-50	34.5	363.0**
	(iii)	233**	133**	1214.5**	998**	-19.5	-1885.0**
	(iv)	231**	-257**	912.0**	574**	782.0**	-990.0**
Seed yield per plant	(i)	112.7**	147.2**	479.0**	384.8**	122.9*	-554.7**
	(ii)	223.6**	-100.1**	418.2**	165.8	-93.8*	-121.1
	(iii)	171.9**	-47.7**	288.3**	235.4*	-75.4*	-425.4**
	(iv)	126.1**	-173.1**	523.1**	441.0**	-190.2*	-774.1**

* Significant at 5 per cent probability level
** Significant at 1 per cent probability level.

(i)+ = $RS_1 - O_m \times RN_1 - O_m$
(ii) = $RS_1 - O_m \times RT_1 - 2_m$
(iii) = $RS_1 - O_{wm} \times RN_1 - O_{mb}$
(iv) = $RN_1 - O_{mb} \times RN_1 - O_m$

Number of pods per plant
    A high degree of heterosis and over-dominance was observed for number of pods per plant. The F_1 plants were significantly ($P = 0.01$) higher than the better parent in all the crosses. In the cross RS_1 - $O_{wm} \times RN_1$ - O_{mb}, the maximum percentage increase over the parents was 141 per cent heterosis and 120 per cent over-dominance. In gene action for number of pods per plant, the estimates of additive gene effects were positive

and better parent was observed for seed yield. A maximum of 168 per cent heterosis and 157 per cent over-dominance were recorded for RS_1 - $O_m \times RT_1$ - 2_m, and a minimum heterosis of 34 per cent and over-dominance of 14 per cent were recorded for RS_1 - $O_{wm} \times RN_1$ - O_{mb}. Estimates of the additive gene effects in seed yield per plant were highly significant, but negative in three crosses (Table 3). Dominance gene effects in all the crosses were positive, highly significant, and of magnitudes comparable to the F_2 mean. The additive × additive type of epistasis was positive in all the crosses, highly significant in crosses (i) and (iv), and significant in cross (iii). The additive × dominance gene effects had negative signs, except in cross

(i) which had a positive sign. The dominance × dominance gene effects were highly significant in crosses (i), (iii) and (iv). The values were, however, negative.

Discussion

Heterosis has been defined as the superiority of an F_1 hybrid over its better parent (Mather, 1955) or at least over the mean of the two parents (Leng, 1954; Quinby, 1970; Walton, 1971). For both definitions, substantially beneficial hybrid vigour was shown for the two traits studied in all the crosses. The magnitude of the increase of the F_1 hybrid in the number of pods and seed yield per plant over the parents showed that provided there are possibilities of hybrid seed production, and other things being equal, the F_1 could be used directly by castor growers to ensure high and stable yields. The F_1 would thus provide planting materials with substantial pod and seed production potentials. However, this does not preclude the possibility of selecting and advancing superior individual plants from the backcrosses, the F_2, and subsequent segregating populations.

Although the estimates of the additive gene action were highly significant, their effects were negative in most of the crosses. This tends to suggest minimal contribution of additive gene effect particularly in seed yield per plant. Contrarily, earlier reports on grain yield of corn (Robinson, Comstock & Harvey, 1955) have shown that additive gene effects made major contributions to total genetic variation. The discrepancy can be explained from two view points. Firstly, the authors assumed negligible epistatic gene effects in their genetic model. This may have caused an upward bias in the estimate of additive genetic variance. Secondly, the values of additive gene effects are expected to be larger whenever randomly mated inbred lines are used as parents. It is likely that the artificial selfing of the parental lines before hybridization reduced the values of the additive gene effects.

The contributions of dominance gene effect to variations in the crosses are shown by the relative magnitude of the dominance component of variation to the F_2 mean. The highly significant dominance gene effects in all the crosses implicate the dominance gene component as a major contributor to the variations in the two metric traits. This reinforces earlier reports (Narkhede et al., 1987) which implicated dominance gene action in the inheritance of seed yield in castor.

The magnitude of the epistatic gene effects, additive × additive, additive × dominance, and dominance × dominance in some of the crosses were high enough to be potentially important as reported by Hayman (1958). When considered on individual basis, the additive × additive type of epistasis appears to have contributed more meaningfully as the effects were positive and significant in most of the crosses. The effects of the additive × dominance epistasis appear to be low. Though dominance × dominance epistasis was highly significant in all the crosses, its value was essentially negative. This is expected because of the high heterotic value associated with the F_1 population, as dominance × dominance gene effects do not contribute to heterotic performance (Gamble, 1962).

According to Mather & Jinks (1971), when dominance and dominance × dominance gene effects have the same sign, the interaction is of the complementary type, but when they have opposite signs, interaction is of the duplicate type. The complementary type of epistasis is therefore present only in cross (ii) for number of pods per plant. The other crosses showed duplicate interaction in the two traits, number of pods per plant, and seed yield per plant.

The results of the study showed that additive gene effects were more relevant in determining number of pods per plant. Thus, the improvement of the character can be enhanced with any breeding method that would encourage the concentration of genes for number of pods per plant. The indeterminate podding habit of the castor plant would suggest the use of the reciprocal recurrent selection as the most effective.

The significant dominance gene effects on number of pods per plant indicate that pod yield in castor plant can also be improved by hybridization. Similarly, the significant dominance gene effects on seed yield per plant implicate hybridization as a breeding method for improving the trait. Thus, reciprocal recurrent selection and the use of hybrid programmes are the breeding strategies suggested for improving pod and seed yield in castor plant.

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