Generation mean analysis for forage yield and quality in Kenaf

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Abstract

The objective of this study was to estimate heritability, heterosis, and genetic parameters involved in the control of forage yield and quality in kenaf populations, using analysis of generation means. Two crosses were used; Cuba 2032×Accession 75-71 and IX51×Everglade 41. Experimental material comprised of P_1 and P_2, their F1 and F2 and BC1P1 and BC1P2 generations. The effects of generations were significant for all traits in both crosses. Results revealed that both additive and non-additive effects were important for the inheritance of the traits in both crosses. The additive gene effects had a higher contribution than dominance gene effects, for most of the traits in cross 1, while dominance gene effects had a greater contribution than additive gene effects, for most of the traits in cross 2. Broad-sense heritability was high for the majority of traits in two crosses, while narrow-sense heritability was higher in cross 1 than in cross 2 for all traits. In cross 2, heterosis estimates were higher than those of cross 1 for most of the traits. Thus, selecting the segregating generations would lead to a significant improvement for forage yield.

Key words: Additive, Dominance, Gene effect, Kenaf.

INTRODUCTION

Kenaf (*Hibiscus cannabinus* L.) belongs to the Malvaceae family and is an annual herbaceous crop native to central Africa. It has a wider range of adaptation to climatic and soil conditions compared to other fiber plant species grown for commercial use. It is grown in many countries for fiber, but has found potential as a source of feed for ruminant animals (Webber and Bledsoe, 2002). Kenaf is generally classified as a self-pollinating crop although the structure of the flowers makes it accessible to insects. Thus, with plenty of insects, cross pollination takes place (Jones *et al.*, 1955).

The various components of the kenaf plants contain usable portions like fibers and fiber strands in stems, protein in leaves and oil in seeds. Among kenaf components, leaves possess the highest protein content, which is important for forage production (Webber *et al.*, 2002; Sanchez *et al.*, 2010). Kenaf is a good candidate for high quality livestock forage, due to its high protein content. Nevertheless, the yield and quality have not been evaluated in hybrid kenaf programs for forage production (Nielsen, 2004).

Optimum harvesting time for kenaf as a forage crop is at the early flowering, when plants are about six to eight weeks old (Mohd Najib *et al.*, 2003). Kenaf has to be harvested at an early stage of growth, between 40

– 80 days after planting, to obtain high crude protein (CP) and optimal dry matter (DM) yield (Webber 1990). The percentages of leaf biomass and CP protein decrease as the plant increases in height and maturity. Webber (1993) reported that leaf yield decreased significantly 120 days after planting.

Genetic studies using generation means analysis (GMA) is the first step in producing basic generations. Genetic analysis of quantitative traits based on means and variances of basic generations can be used to estimate the degree of similarity or differences among related individuals and families using standard statistical models. Some statistical genetic models have been devised for plants and animals to estimate the parameters of genetic components (Kearsey and Jinks, 1968; Mather and Jinks, 1982; Chalh and El Gazzah, 2004). However, the choice of an efficient breeding program depends on the available knowledge on the gene function involved in the expression of the character. Dominance gene action would favor the production of hybrids, while additive gene action indicates that standard selection procedures would be effective in the breeding program (Azizi *et al.*, 2006). There is little genetic information or breeding efforts for improving genotypic characteristics of kenaf as forage and no study has been conducted to estimate the genetic control of kenaf forage yield, the proportion of additive, dominance and epistatic gene effects. Therefore, the present study was conducted to estimate genetic parameters for forage yield and quality using generation means analysis.

MATERIALS AND METHODS

Plant materials and location of experiment
Four cultivars including Cuba 2032, Accession 75-71, IX51 and Everglade 41 were selected as parents in this study. Cuba2032 and IX51 were chosen for their high yield, while accession 75-71 and Everglade 41 were chosen for their high CP content. The two crosses were Cuba 2032 (P_1)×Accession 75-71 (P_2) (cross 1), and IX51 (P_1)×Everglade 41 (P_2) (cross 2). In each cross, the high yielding parent (P_1) was crossed to the parent with a high CP content (P_2) to produce F_1 seeds. Selected parental seeds of each cross and their F_{1s} were then planted in the field to perform further crosses. These F_1s were crossed to their parents P_1 and P_2 to get BC_1P_1 and BC_1P_2 generations, respectively. The F_1 plants were also allowed to self-pollinate to produce F_2 seeds. Sufficient seeds of all generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were produced from cross 1 and cross 2 under field conditions with controlled pollination. Basic generations for the two crosses were planted separately in Field 10, University Putra Malaysia, Serdang, Selangor, Malaysia, on January 2010 (2º 59' N, 101º 42' E, 12 m above the sea level. The basic generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) from each cross were evaluated separately in a randomized complete block design (RCBD) with three replications.

Field practices and data collection
Seeds were planted by hand. Planting arrangement of 76×7 cm between and within rows was used in all plots. The number of rows was four for each of the non-segregating generations (P_1, P_2 and F_1 generations), five for each backcross generation and six for the F_2 generation. The compound fertilizer, Nitrophoska Green (N: P: K: 15:15:15) was applied at the rate of 90 kg ha^{-1} (N), 90 kg ha^{-1} (P_2O_5), and 90 kg ha^{-1} (K_2O), where half of the fertilizer was applied before planting and the rest was applied one month later. Lasso (2-chloro-2'-6'-diethyl-N-methoxymethyl) was used at the rate of two tons ha^{-1} as pre-emergence herbicide. Weeds in the plots were controlled by hand-weeding during the growing season. The experimental field was irrigated using the overhead sprinkler system whenever necessary. All cultural practices were the same for both crosses. Measurements were recorded from 21 plants of the P_1, P_2 and F_1 generations, 150 plants of the F_2 and 45 plants of the backcross generations (BC_1P_1 and BC_1P_2) of each cross.

Analysis of generations means
Data were first tested for skewness, kurtosis and normality. Then the statistical analysis for generation means was conducted using the computer software MINITAB version 14 (Minitab, 2005) to estimate gene effects following the method described by Mather and Jinks (1982):

(1) $Y= m + \alpha[a] + \beta[d] + \gamma^2[i] + 2\alpha\beta[j] +\beta^2 [l]$

Where,

Y=generation mean,

M=mean of all possible homozygous lines which can be derived from a cross,

α and β=coefficients of genetic parameters,

[a]=additive gene effects,

[d]=dominance gene effects,

[i]=additive×additive gene effects,

[j]=additive×dominance gene effects, and

[l]=dominance×dominance gene effects.

In the generation means analysis, the additive-dominance model was first subjected to the weighed least squares analysis using the joint scaling test to verify the goodness of fit of the model (Kearsey and Pooni, 2004), where

(2) $\quad$ Weight (wt_i) = Generation size (n_i) / Variance (S_i^2)

The best model was the one which showed significant estimates of all parameters along with the non-significant chi-squared values (Kearsey and Pooni, 2004). The potency ratio or dominance effect (DE) was calculated using the method of Smith (1952):

(3) $\qquad D.E. = \dfrac{\overline{F1} - \overline{MP}}{\frac{1}{2}(\overline{P2} - \overline{P1})}$

Where F1=mean value of the hybrid; MP=mid-parent; P2=mean of the highest parent; and P1=mean of the lowest parent.

Heritability estimates
Broad-sense heritability (h^2_B) and narrow-sense heritability (h^2_N) estimates were calculated using the formula described by Kearsey and Pooni (2004), as follows:

(4) $\qquad h^2_B = (V^*_A + V^*_D) / (V^*_A + V^*_D + V_E)$

(5) $\qquad h^2_N = (V^*_A) / (V^*_A + V^*_D + V_E)$

The genetic variance (V_G) and environmental variance (V_E) were estimated using the within-generation variances of the F_2 and non-segregating generations. The $*$ notation in variances V^*_A and V^*_D is to distinguish the special case of equal allele frequencies (Kearsey and Pooni, 2004).

Heterosis was quantified as the deviation of the F_1 value from the mid-parent (MP) value (Coors, 1999) as follows:

(6) $\qquad MPH = \dfrac{\overline{F_1} - \overline{MP}}{\overline{MP}} \times 100$

Inbreeding depression was estimated using the following equation:

(7) $\qquad$ Inbreeding depression $= \dfrac{\overline{F_1} - \overline{F_2}}{\overline{F_1}}$

RESULTS

Analysis of variance revealed significant differences among the generations for all traits. Therefore, the analysis of generation means was employed to estimate genetic parameters for the traits. Mean performances, standard error of the basic generations for the traits and potency ratio in cross 1 and cross 2 are presented in Tables 1 and 2, respectively. The results indicated that mean performance of the F_1 was higher than the mid-parental value for all traits, except for days to flowering in both crosses. Potency ratio was more than one for stem-ADF in cross 1 (2.26) and it was less than minus one for leaf to stem ratio in Cross 2 (-2.91), indicating the presence of over dominance for these traits.

Estimates of genetic parameters for the traits are presented in Tables 3 and 4 for cross 1 and cross 2, respectively. The non-significant Chi-square values obtained from the joint scaling tests indicate that three parameters of the model were adequate to explain the variability for plant DM yield and stem DM yield in Cross 1. However, significant Chi-square values for other traits in cross 1 and all traits in cross 2 indicate that the three parametric models were not adequate to explain the existing variability. Therefore, a six parametric model ([m], [a], [d], [i], [j] and [l]) was fitted for these basic generations.

Given the fact that χ^2 value was almost zero, a six parameter model could be suitable. Therefore, epistatic gene effects play an important role in the inheritance of these traits. In cross 1, the five parametric model was fitted for plant height, leaf-CP and stem-CP contents, and the four parametric model was fitted for leaf DM yield, days to flowering, leaf-ADF and leaf to stem ratio. In cross 2, the five parametric model was fitted for plant DM yield, leaf DM yield, stem DM yield, plant height, leaf-CP content, stem-CP content and leaf-ADF and the four parametric model was fitted for stem-ADF and days to flowering.

In the present study, the additive gene effects were significant for all traits in both crosses. The dominance gene effects were also significant for all traits in both crosses, except for leaf to stem ratio and leaf-ADF in cross 1 and stem-ADF in cross 2 which were not significant. This indicated that dominance gene effects play an important role in controlling the genetic variation in these traits. However, the relative contribution of dominance gene effects was higher than the additive gene effects in cross 2 for all the studied traits, except for leaf-CP, stem-ADF and days to flowering.

The additive×additive [i] type of epistatic gene effects were positive and significant for leaf DM yield and plant height, but was negative and significant for leaf-CP content, stem-ADF and days to flowering in cross 1. However, in cross 2, epistatic gene effect

Table 1. Mean performances (±standard error) of the basic generations for studied traits in Cross 1 (Cuba 2032×75-71).

Generation	Mean									
	Plant DM yield (g plant⁻¹)	Leaf DM yield (g plant⁻¹)	Stem DM yield (g plant⁻¹)	Plant height (cm)	Leaf to stem ratio (%)	Leaf-CP content (%)	Stem-CP content (%)	Leaf-ADF (%)	Stem-ADF (%)	Days to flowering
Cuba 2032 (P₁)	87.9^a±2.7	27.5^a±0.7	60.5^a±0.8	275.7^a±2.8	46.2^b±1.0	19.6^d±0.2	2.7^c±0.2	25.0^a±0.2	60.4^{bc}±0.6	90.0^a±0.0
75-71 (P₂)	35.4^c±1.5	5.8^d±0.4	19.6^d±0.9	138.4^c±2.6	62.7^a±3.2	26.0^a±0.3	5.8^a±0.2	22.5^b±0.2	62.3^{ab}±0.6	54.0^d±0.0
F₁	65.9^b±1.4	24.9^a±0.6	41.0^b±1.1	242.2^b±1.3	51.4^b±1.6	23.4^b±0.4	4.4^b±0.2	24.2^a±0.4	63.5^a±0.5	67.0^c±0.0
F₂	56.0^b±2.9	18.4^b±1.1	37.7^b±1.9	213.3^b±4.1	51.0^b±1.2	20.6^{cd}±0.3	4.0^c±0.2	23.7^a±0.2	62.1^{ab}±0.7	78.3^b±1.4
BC₁P₁	68.7^b±4.8	22.4^{ab}±1.7	46.2^b±3.2	249.1^{ab}±4.3	49.5^b±1.8	17.8^e±0.3	3.4^c±0.2	24.2^a±0.4	57.6^b±0.7	81.5^b±1.8
BC₁P₂	38.9^c±3.1	12.6^c±1.0	26.3^c±2.2	198.8^c±5.44	49.2^b±1.6	21.7^c±0.5	2.6^c±0.2	24.1^a±0.3	63.1^a±0.5	65.0^c±1.9
Potency ratio	-0.16	-0.76	-0.05	-0.51	-0.37	0.19	0.10	-0.36	2.26	0.28

Means with the same letter within a column are not significantly different at p≤0.05.

Table 2. Mean performances (±standard error) of the basic generations for studied traits in Cross 2 (IX51×Everglade 41).

Generation	Mean									
	Plant DM yield (g plant⁻¹)	Leaf DM yield (g plant⁻¹)	Stem DM yield (g plant⁻¹)	Plant height (cm)	Leaf to stem ratio (%)	Leaf-CP content (%)	Stem-CP content (%)	Leaf-ADF (%)	Stem-ADF (%)	Days to flowering
IX51 (P₁)	60.3^a±0.4	22.8^a±0.3	37.5^a±0.3	229.5^a±0.9	62.4^b±2.0	20.9^a±0.3	3.6^c±0.3	22.5^c±0.3	63.4^{ab}±0.5	81.0^a±0.4
Everglade 41 (P₂)	26.4^d±0.8	9.2^d±0.4	17.1^{cd}±0.5	169.4^d±1.4	53.8^c±0.9	28.9^a±0.3	6.2^a±0.3	24.0^{ab}±0.2	60.8^c±0.5	56.5^d±0.5
F₁	49.1^b±1.1	20.2^b±0.5	28.9^b±0.8	185.1^c±1.2	70.6^a±2.4	27.6^b±0.8	5.3^b±0.4	24.4^a±0.4	62.7^b±0.5	70.6^b±0.5
F₂	26.0^d±0.8	10.9^d±0.4	15.8^d±0.5	165.2^d±1.4	66.2^{ab}±2.1	27.5^b±0.8	4.6^b±0.4	22.8^b±0.4	62.9^b±0.5	62.13^b±0.6
BC₁P₁	44.7^b±3.6	14.2^c±1.1	30.5^b±2.6	217.1^b±5.7	48.7^c±1.7	25.8^c±0.3	5.1^b±0.2	23.3^{bc}±0.3	64.8^a±0.5	72.8^b±2.7
BC₁P₂	35.6^c±1.5	14.1^c±0.7	21.4^c±0.9	171.1^d±1.5	66.3^{ab}±1.8	27.8^{ab}±0.4	5.0^b±0.2	23.0^c±0.2	61.0^c±0.4	57.8^{cd}±1.2
Potency ratio	-0.34	-0.62	-0.16	-0.48	-2.91	0.68	0.31	1.53	-0.46	-0.15

Means with the same letter within a column are not significantly different at p≤0.05.

Table 3. Estimates of genetic parameters (± standard error) for 14 studied traits based on the six-parameter model in Cross 1 (Cuba 2032×75-71).

Trait	m	a	d	i	j	l	X^2
Plant DM yield	50.83±1.37**	35.55±1.38**	14.45±1.99**	-	-	-	3.44ns
Leaf DM yield	10.06±1.98**	10.81±0.39**	14.71±2.26**	6.52±2.03**	-	-	3.3ns
Stem DM yield	34.49±1.14**	24.85±1.15**	6.43±1.64**	-	-	-	1.91ns
Plant height	189.35±7.24**	68.64±1.89**	53.03±7.66**	17.97±7.59*	-33.64±14.04*	-	1.5ns
Leaf to stem ratio	54.44±1.74**	1.22±0.18**	0.39±0.38ns	-	-2.44±1.07*	-	1.73ns
Leaf-CP	26.86±1.67**	-3.29±0.20**	-21.54±4.04**	-4.04±1.65*	-	18.06±2.52**	1.12ns
Stem-CP	4.24±0.21**	-1.55±0.21**	-4.89±0.78**	-	4.76±0.70**	5.02±0.71**	0.49ns
Leaf-ADF	23.73±0.18**	1.22±0.18**	0.39±0.38ns	-	-2.44±1.07*	-	1.73ns
Stem-ADF	68.54±2.67**	-0.98±0.45*	-20.94±7.45**	-7.21±2.63**	-8.92±2.44**	15.64±4.91**	0.00
Days to flowering	88.98±2.51**	17.99±0.29**	-21.99±2.60**	-16.97±2.53**	-	-	0.56ns

m=mean; [a]=additive gene effect; [d]=dominance gene effect; [i]=additive×additive gene effect; [j]=additive×dominance gene effect; [l]=dominance×dominance gene effect; *, ** and ns=significant at p≤0.01, p≤0.05 and non-significant, respectively.

Table 4. Estimates of genetic parameters (± standard error) for 14 studied traits based on the six-parameter model in Cross 2 (IX51×Everglade 41).

Trait	m	a	d	i	j	l	X^2
Plant DM yield	-24.00±6.37**	15.66±1.61**	126.76±17.83**	66.18±6.66**	-53.70±11.75ns	-	3.33ns
Leaf DM yield	0.16±0.90ns	6.80±0.64**	20.02±1.30**	15.88±1.12**	-13.53±2.52**	-	0.01ns
Stem DM yield	-15.05±3.98**	10.01±1.09**	79.43±11.18**	42.21±4.24**	-35.50±7.41**	-	0.14ns
Plant height	70.16±8.31**	45.10±1.06**	265.05±21.42**	114.30±8.38**	-	-150.17±13.53**	0.02ns
Leaf to stem ratio	88.77±9.70**	4.28±1.37**	-76.19±22.42**	-30.69±9.61**	-43.63±5.45**	57.99±13.74**	0.00
Leaf-CP	27.57±0.80**	-4.03±0.192**	-0.106±1.40*	-2.69±0.81**	4.2±1.07*	-	0.07ns
Stem-CP	3.65±0.44**	-1.27±0.21**	1.91±0.76*	1.28±0.46**	2.73±0.67**	-	1.47ns
Leaf-ADF	21.16±0.43**	-0.75±0.21**	3.15±0.71**	2.05±0.47**	2.24±0.77**	-	0.16ns
Stem-ADF	62.37±0.37**	1.40±0.44**	0.74±0.69ns	-	4.70±1.59**	-	1.35ns
Days to flowering	63.91±1.11**	12.27±0.27**	-3.28±1.37*	4.85±1.15**	-	-	3.39ns

m=mean; [a]=additive gene effect; [d]=dominance gene effect; [i]=additive×additive gene effect; [j]=additive×dominance gene effect; [l]=dominance×dominance gene effect; *, ** and ns=significant at p≤0.01, p≤0.05 and non-significant, respectively.

(additive×additive) was also positive and significant for plant DM yield, leaf and stem DM yields, plant height, stem-CP content, leaf ADF and days to flowering, but it was negative and significant for leaf to stem ratio and leaf-CP content. In cross 1, the additive×dominance [j] gene effect was significant and positive for stem-CP content, but it was negative for plant height, leaf to stem ratio, leaf-ADF and stem-ADF. In cross 2, additive×dominance [j] gene effect was also significant and negative for plant and leaf DM yields, stem DM yield and leaf to stem ratio, while a positive and significant additive×dominance [j] gene effect was revealed for leaf and stem-CP contents, leaf and stem-ADFs. The dominance×dominance [l] gene effect was significant for leaf and stem-CP contents and stem-ADF in cross 1, while a positive and significant dominance×dominance [l] gene effect was found for leaf to stem ratio in cross 2. In addition, it was negative and significant for plant height in cross 2.

The estimates of broad-sense heritability, narrow-sense heritability, heterosis and inbreeding depression are presented in Table 5 for both crosses. The estimates of heterosis and inbreeding depression together provide information about the type of gene action involved in the expression of various traits. The broad-sense heritability estimates ranged from 62.3% (in stem-CP content) to 98.9% (in days to flowering) in cross 1, while it ranged from 19.2% (in leaf-CP) to 99.3% (in days to flowering) in cross 2. The narrow-sense heritability estimates ranged from 37.0% (in stem-ADF) to 98.4% (in days to flowering) in Cross 1, and 8.4% (in leaf-CP) to 76.4% (in days to flowering) in cross 2. The estimates of narrow-sense heritability were found to be high for most of the traits in cross 1, while it was moderate to low for all traits in Cross 2.

Heterosis related to mid-parental values was found to be highest for leaf DM yield (49.7% and 25.8% in Cross 1 and 2, respectively). Heterosis was positive for all traits, except for leaf to stem ratio and days to flowering in Cross 1 and for plant height in cross 2, which was negative in both crosses.

The inbreeding depression estimates ranged from -16.9% (for days to flowering) to 26.2% (for leaf DM yield) in cross 1, and -2.6% (for days to flowering) to 49.6% (for leaf DM yield) in cross 2. Inbreeding depression was found to be positive for all traits, except for days to flowering in crosses 1 and 2 and stem-ADF in cross 2. Negative inbreeding depression implies that F_2 possesses higher values than F_1. In other words, plants that flowered early are more suitable for forage utilization because early flowering hybrids contain

Table 5. Estimates of broad- ($h2B$) and narrow- ($h2N$) sense heritability, mid-parent heterosis and inbreeding depression in the crosses.

Trait	Cross 1				Cross 2			
	h^2_B (%)	h^2_N (%)	Mid-parent heterosis (%)	Inbreeding depression (%)	h^2_B (%)	h^2_N (%)	Mid-parent heterosis (%)	Inbreeding depression (%)
Plant DM yield	94.6	89.0	6.89	15.0	91.4	45.9	13.2	47.1
Leaf DM yield	96.2	43.7	49.7	26.2	84.2	38.9	25.8	49.6
Stem DM yield	91.1	85.7	2.37	8.2	92.4	47.1	5.7	45.3
Plant height	96.8	82.8	17.0	11.9	98.1	42.9	-7.19	10.8
Leaf to stem ratio	67.3	48.4	-5.6	0.07	94.5	34.3	21.5	7.6
Leaf-CP	91.5	73.5	2.4	11.9	19.2	8.4	10.8	0.2
Stem-CP	62.3	45.9	2.9	13.6	37.2	10.2	8.5	13.4
Leaf-ADF	65.0	53.8	1.9	18.8	61.8	27.3	4.9	6.6
Stem-ADF	88.6	37.0	3.6	2.2	29.5	21.4	1.0	-0.2
Days to flowering	98.9	98.4	-6.9	-16.9	99.3	76.4	2.69	-2.6

high CP contents , and therefore, it is possible to apply a hybrid breeding program for this trait.

DISCUSSION

Analysis of variance revealed a significant variation among the generations for different traits in both crosses. Since generations revealed significant variations for traits, analysis of generation means was used to study the genetics of the traits. Significant differences have also been reported for various traits among the generations in cotton (Ahmad, 2009) and maize (Shahrokhi *et al.*, 2011).

As expected, the F_1 mean performance for most of the studied traits was higher than the mid-parental value, indicating the importance of dominance gene effects on the traits control, in the direction of the better parent. Similar results were reported by Abd-El *et al.* (2010) and Dawwam *et al.* (2009) in cotton. These results were in contrast to those of Adeniji and Kehinde (2003), who reported that F_1 mean estimates were not higher than the mid-parental values in West African okra.

The joint scaling test showed that simple additive-dominance model was adequate for explaining the manifestation of plant and stem DM yields in cross 1, indicating the absence of non-allelic interactions in the inheritance of these traits. In a study on genetic control of fiber yield and quality of kenaf by Behmaram *et al.* (2014), the additive-dominance model was adequate to explain genetic control of stem DM yield. The additive-dominance model was adequate to explain genetic control of some traits in okra (Adeniji and Kehinde, 2003) and cotton (Abd-El *et al.*, 2010). They reported that there was not a non-allelic interaction and that the additive-dominance model was adequate to demonstrate the genetic variation and its importance in the inheritance of the traits.

Results of the GMA indicated that additive, dominance and epistatic gene effects were significant for most of the traits in both crosses, indicating that both additive and non-additive effects were important for the inheritance of most of the traits. The same result was reported by Behmaram *et al.* (2014) for some traits on two kenaf populations.

The additive gene effects were higher than the dominance gene effects in cross 1. Maximum utilization of additive gene effects can be obtained by selection after each generation of selfing. Meanwhile, the magnitude of dominance gene effects was higher as compared to additive gene effects in most of the studied

traits in cross 2. This indicated the preponderance of dominance gene effects in controlling the inheritance of these traits. In contrast, in comparison to additive gene effects higher dominance gene effects were also reported by Abd-El *et al.* (2010) on Egyptian cotton varieties. Esmail (2007) explained that when the non-additive effects are higher than the additive effects, the improvement of the characters needs intensive selection through later generations.

The negative and significant dominance gene effects [d] in leaf and stem-CP contents, stem-ADF and days to flowering in cross 1, and leaf to stem ratio, leaf-CP content and days to flowering in cross 2, implied that the inheritance of these traits have tendency towards the lower parent. The negative and significant dominance gene effects [d] for most studied traits were also observed in okra (Adeniji and Kehinde, 2003). Positive sign of [d] suggested its enhancing effect on the performance of most traits in both crosses.

Epistatic gene effects were found to be important for the inheritance of all traits in both crosses, except for plant DM yield and stem DM yield in cross 1, in which a three parameter model was adequate to explain the variability for those traits. Additive×Additive gene effects [i] were positive for most of the studied traits in both crosses, suggesting that selection should be carried out in later generations and the interaction should be fixed by selecting under selfing conditions. A highly significant Additive×Additive gene effect [i] was reported by Abd-El *et al.* (2010) in some Egyptian cotton varieties.

Additive×Additive gene effects [i] were negative for leaf-CP content, stem-ADF and days to flowering in cross 1, and for leaf to stem ratio and leaf-CP content in cross 2. This implies that genes with negative additive actions existing in parents need to be eliminated in the early segregating generations. Negative additive× additive gene effects [i] were also reported in okra by Adeniji and Kehinde (2003). The significant negative additive×dominance [j] gene effects were observed for some traits, except for stem-CP content in cross 1, and for leaf and stem DM yields and leaf to stem ratio in cross 2, suggesting the dispersion of genes in the parents. The opposite signs of [a] and [i] for days to flowering in cross 1 and for leaf to stem ratio, stem-CP and leaf-ADF in cross 2 may present opposite natures for these traits.

The opposite signs of [d] and [l] for leaf-CP, stem-CP and stem-ADF in Cross 1 and for plant DM and leaf DM yields, stem DM yield and leaf-CP in cross 2 suggested a duplicate type of epistasis which will

pose hindrance to a plant breeder while attempting selections in long run.

The results of potency ratio showed over dominance for stem-ADF and leaf to stem ratio in cross 1 and 2, respectively. This was in agreement with low narrow sense heritability for these traits. Selection of these traits must therefore be delayed until the F3 or F4 generation. This delay permits a loss of non-additive genetic variances through inbreeding, so that the additive genetic variances can be evaluated more clearly (Said, 2014). The additive portion, which is reflected in the narrow sense heritability, reflects the degree to which progenies are likely to resemble their parents. Plant breeders implore the knowledge of heritability in making decisions on which genetic improvement is possible through selection (Falconer, 1981). High values of narrow-sense heritability estimated for half of the traits in cross 1 indicated that selection for these traits is likely to be successful.

Behmaram *et al*. (2014) reported higher broad- and narrow-sense heritabilities in population 1 compared to population 2 for all traits except for bast (outer bark) percentage on two kenaf populations. Liu (2005) reported a high broad-sense heritability for yield and yield related traits. It indicated that the phenotypic variation due to environmental variation was limited in these traits. High broad-sense heritability for plant height and some other studied traits was also reported among Roselle genotypes (Ibrahim and Hussein, 2006).

High broad-sense heritability and moderately low narrow-sense heritability were revealed for most of the traits in cross 2. In a study on diallel and stability analysis of kenaf reported by Liu (2005), low narrow-sense heritability was found for all studied traits. Falconer and Mackay (1996) reported that low narrow-sense heritability was caused by low additive and high dominance gene effects.

Positive heterosis indicated the importance of hybrid vigour for the traits, but negative heterosis indicated that dominance was in the direction of the parent with lower values heterosis estimates were higher in cross 2 than those of cross 1 for most of the traits, indicating that the level of additive and dominance gene effects was different in the parents for most of the traits in two crosses. Therefore, hybrids produced from parents with higher gene effects may contribute more to heterosis. High heterosis for yield related traits was reported by Liu (2005) on kenaf. This indicates that a considerable potential exists in the germplasm to be used for developing hybrids. However, negative heterosis was reported for days to flowering, first fruiting and

branches per plant in all crosses in cotton varieties, indicating that hybrids flowered and produced fruits earlier than parents (Abd-El *et al.*, 2010). In contrast, in a study on genetic control of fiber yield and quality, positive heterosis was reported for days to flowering in two kenaf populations (Behmaram *et al*., 2014).

Inbreeding depression, broad-sense heritability and narrow-sense heritability estimates were also largely different between two crosses. Inbreeding depression was positive for all studied traits, except for days to flowering in cross 1, and stem-ADF and days to flowering in cross 2. This was expected, as the expression of heterosis in the F_1 generation was followed by a reduction in performance in F_2 due to an increase in homozygosity. Plant yield had a high ID, indicating that yield was controlled by a higher number of genes. Agarwal and Shrotria (2005) reported that the hybrid combinations that showed higher estimates of heterosis, in general found to show substantial IDs. Positive ID in forage sorghum was also reported for fresh plant and plant DM yields (Bhatt, 2008). Positive ID was reported by Abd-El *et al.* (2010), in Egyptian cotton varieties. The negative ID for those mentioned traits in cross 1 and cross 2 may be attributed to the occurrence of transgressive segregation in the F_2 generation. The formation of new gene combination as a result of segregation may lead to an increase in the expression of the traits in F_2 generation. In the crosses showing negative and significant IDs, there is a scope for the selection of plants in F_2 generation for improving the desirable traits.

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