Genetic Control of Fiber Yield and Quality in Kenaf (*Hibiscus cannabinus* L.)

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ABSTRACT

The study was conducted to investigate the genetic basis of kenaf fiber yield and quality In two sets of generations derived from 1X51 x Ghana07 and Gregg x Ghana07 crosses. Analysis of generation means using weighted least squares procedure was performed on stalk dry weight, bast percentage, days to flowering, plant height, and basal stalk diameter . Analysis of generation means revealed that bast percentage was mainly controlled by dominance effects whereas stalk dry weight was mainly controlled by additive effects. Estimates of heterosis based on mid-parental values were generally high and ranged from 10 to 55% for stalk dry weight and bast percentage. Estimates of inbreeding depression, calculated from F_1 and F_2 generation means, were 55% for stalk dry weight in Population 1 and 43% in Population 2. Estimates of inbreeding depression for bast percentage were 5% in Population 1 and 15% in Population 2. The results of this study indicated that the portion of phenotypicvariations,which is controlled by additive gene effects, was generally high for stalk dry weight. Thus, selectingthe segregating generations would lead to significant improvement of fiber yield.

Keywords:genetic analysis, generation mean analysis,kenaf fiber yield, heritability, additive effect, dominance effect.

INTRODUCTION

Renewable resources for bio-composite products in the world are essential. Kenaf (*Hibiscus cannabinus*L.) has been considered as a potential renewable source for the bio-composite industry in the world. World production of kenaf and allied fibers was 3,251,125 tons in year 2009 (FAO, 2011).

Kenaf has a chromosome number in multiples of 18, with 2n=36 to 2n=180 (Wilson, 2003; Coetzee, 2004). The flowers are adapted both for cross- and self-pollination (Pate and Joyner, 1958), although cross-pollination is a consequence of insect activity (Jones *et al.*, 1955). It was also found that outcrossing rate was only 2 to 24%. The main product of kenaf is the stalk which contains two types of fibers: long fibers that produce high quality paper and short fibers that produce low quality paper. Many reports about kenaf productivity have been published from works in Australia (Carberry and Muchow, 1992; Carberry *et al.*, 1992), USA (Webber *et al.*, 2002) and other countries (Coetzee *et al.*, 2008, 2009). Through an experiment in Australia, Carberry*et al.*(1992) reported that kenaf stem yield ranged from 4.5 to 19.2 t ha^{-1}. Based on a report from Meints and Smith (2003) biomass yields ranged from 12.39 to 14.57 t ha^{-1} in year 1999 and 16.82 to 18.47 t ha^{-1} in year 2000 in USA. In a study in Malaysia on 40 kenaf accessions in sandy soil, the highest dry mass accumulation in the stem was reported to be 66.5 g $plant^{-1}$ for acces-

sion C75 (Hossain *et al.,* 2012). Bahtoee *et al.* (2012) reported that Cultivar 7552 produced the highest amount of fiber (2641 kg ha^{-1}) among nine cultivars in Iran.

Kenaf breeding programs have not been intensively conducted as it is not considered an important commercial crop of the world. White *et al.* (1994) believed that it remains on the verge of significant commercialization. Limited number of genetic studies on kenaf fiber yield has been reported in the literature. Heterosis for fiber yield is strongly expressed and hybrid kenaf cultivars have been developed and used for commercial production in China (Liu, 2005). Heritability is one of the important genetic parameters which is estimated as broad- and narrow-sense (Falconer and Mackay 1996; Lynch and Walsh, 1998). High heritability estimate of a trait indicates that the trait can be improved through selection for the trait.

Liu (2005) reported very high broad-sense heritability values for all yield related characteristics, including fresh plant mass, defoliated plant mass, plant height and basal stalk diameter, varying from 0.72 to 0.86. No study has been conducted to estimate the genetic control of fiber yield, the proportion of additive, dominance and epistatic gene effects.

Moderate broad-sense heritability value (0.24) for the ratio of bast weight to core weight was reported in kenaf by Liu (2005). High broad-sense heritability values were reported for days to flowering (0.98) and plant height (0.88) by Foroughi (2012).

To-date, no information is reported on kinds and amounts of gene effects involved in the control of kenaf fiber yield and quality. High heterosis for yield characteristics based on mid-parent and better-parent was reported by Liu (2005). A predominantly additive effect was also detected for days to flowering in a diallel analysis of kenaf (Gray et al., 2006).

Several models of generation means analysis procedure have been developed to partition the genetic components of a quantitative trait (Mather and Jinks, 1977, 1982; Jinks, 1979). The generation means analysis procedure has been reviewed recently (Carena *et al.,* 2010). Some limitation of this analysis must also be noted (Carena *et al.,* 2010). Despite its limitations, it has been used popularly in many researches (Saleh and Gritton, 1994; Tefera and Peat, 1997).

General objective of the present study were to establish genetic information for an early breeding program for the improvement of kenaf fiber yield and quality. While the specific objectives of the present study were to: i) determine the additive, dominance and epistatic effects of genes involved in the control of fiber yield and bast percentage, ii) estimate heterosis, inbreeding depression and heritability for fiber yield and bast percentage, and iii) determine correlations among fiber yield and fiber quality traits.

MATERIALS AND METHODS

Parental cultivars and development of populations

Three cultivars including Gregg, 1×51 and Ghana07, were selected as parents in this study based on the results of Foroughi (2012).Characteristics of the studiedcultivars by Foroughi (2012) are shownin Table 1. Gregg and 1×51 were chosen for their high fiber yield, while Ghana07 was chosen for its high bast percentage.

Two study populations were developed. population 1 consisted of 1×51 (P_1), Ghana07 (P_2), and their F_1, F_2, BC_1P_1 and BC_1P_2, generations. population 2 consisted of Gregg (P_1), Ghana07 (P_2), and their F_1, F_2, BC_1P_1 and BC_1P_2 generations.

Initial crosses between the two parents in populations 1 and 2 were made in Field 10, Universiti Putra Malaysia (UPM), Serdang (2^o 59' N, 101^o 42' E, at 48 m above the sea level), in the months of March to July 2009.

Sufficient seeds of P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2 were produced for the populations under field conditions with controlled pollination. To produce the F_1 seeds five plants from the two selected parents were crossed. To produce seeds of the F_2 generations of both populations, 10 randomly selected plants of the F_1 generation were self-pollinated by bagging the flowers. To produce seeds of the BC_1P_1 and BC_1P_2 generations of both populations, five plants from the F_1 and each parent P_1 and P_2 were crossed, respectively. Pedigrees of all individual generations of both populations were tracked by tagging every plant during the population development procedure.

Evaluation of populations and data collection

Each population was evaluated separately in a Randomized Complete Block Design (RCBD) with three replications in Field 10, UPM, Serdang in 2011. All cultural practices and data collection procedures were the same for both populations.

The P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2 generations were the six treatments in the experiments. As F_2 is the most segregating generation, a larger number of F_2 plants should be studied. Therefore, for P_1, P_2, F_1, BC_1P_1 and BC_1P_2, each plot consisted of four 3.5 m long rows, while the F_2 plots consisted of six 3.5 m long rows. Planting arrangement of 35 × 20 cm between and within rows was used in all plots. Each plot

Table1. Mean values for fiber yield and quality characteristics of kenaf cultivars used in the study.

Cultivar	Mean value			
	Bast to core ratio	Stalk dry yield(kg ha^{-1})	Stalk height (cm)	Days toflowering
Gregg	0.54	10001	262	63
1X51	0.49	14468	297	84
Ghana07	0.62	8280	243	75

Source: Foroughi, 2012

was consisted of 70 plants except for the F_2 plots which consisted of 105 plants in each plot.

Plots were irrigated with a sprinkler irrigation system. Weeds were controlled manually. Fertilizers were applied at the rate of 150 kg ha^{-1} N, 120 kg ha^{-1} P_2O_5 and 120 kg ha^{-1} K_2O. Pest control was performed by spraying 2 ml l^{-1}Decis® (deltamethrin) at the initial flowering stage.

Excluding plants from the border rows and ends of the middle rows, 18 individual plants of P_1,P_2 and F_1 generations and 50 plants from the backcross and 150 plants from F_2 generations were randomly taken and tagged for measurements of plant characteristics and yield data. Experimental fields were visited daily to record the initial flowering date of every tagged plant. Days from emergence to the bloom of the first flower of every plant was defined as days to flowering. The tagged plants were harvested 15 days after the first flower bloomed. Plant height, plant fresh weight, and basal stalk diameter were recorded immediately after harvest. Measurements of the traits were taken as follows:

- plant height, measured from the ground level to the last node of the plant,
- plant fresh weight, measured as the weight of whole plant for each sample (single plant) immediately after harvest,
- basal stalk diameter, measured using the Vernier caliper at the base of the stalk,
- bast percentage, measured as proportion of dry bast weight over whole dry stalk weight. To measure dry bast weight and dry stalk weight, leaves were removed from the stalks, and the bast and core of every plant were separated by hand and separately oven dried for 3 days at 70 ^{o}C.Bast percentage of each sample was calculated based on dry weight. The following formula for calculation of bast percentage was used.

Bast percentage (%) = (bast dry weight / stalk dry weight) × 100 Yield were estimated based on whole plots for P_1, P_2 and F_1 generations, whereas harvested single plant means were used to estimate yields for the F_2, BC_1P_1 and BC_1P_2 generations.

Genetic and statistical procedures

Analysis of variance was applied to determine generation and block effects in each population separately on all data. The General Linear Model Procedure (Proc GLM) of the Statistical Analysis System (SAS) computer software (SAS Institute Inc., 2003) was used to perform the ANOVA. As all generation were involved in the experiment, the effects of generation (treatment) were considered as fixed effects.

Pearson's simple correlation coefficients between pairs of traits from data of the F_2 generationwere calculated.

Analysis of generations means

Generation means analysis was carried out for traits that showed significant differences among generations within a population. Generation means analysis and Joint-Scaling Test, which was suggested by Mather and Jinks (1977) and reviewed by Carena *et al.* (2010) was employed in this study. Estimates of gene effects were calculated for stalk dry weight, bast percentage, days to flowering, plant height and basal stalk diameter.

Homozygous and divergent parental cultivars promise the required assumption of generation means analysis. To fulfill the assumptions, parental cultivars with divergent fiber yield and quality were chosen. Before selection, parental cultivars were observed and self-pollinated by bagging flowers for two generations during seed multiplication and preliminary evaluation. Consequently, parental cultivars were selected from the cultivars with no morphological variations assuming that they are homozygous.

If parental cultivars differ by any number of unlinked loci, expectations of parents and their descendant generations in terms of genetic effects relative to the F_2 generation is based on the following model (Carena*et al.*, 2010):

$$Y=m+\alpha_a+\beta_d+\gamma^2_{aa}+2\alpha\beta_{ad}+\beta^2_{dd} \quad (1)$$

where,

'Y'is the observed mean,

'm'indicates overall mean,

'*a*' indicates pooled additive effects across loci,
'*d*' indicates pooled dominance effects across loci,
'*α*'and '*β*'are the coefficients of *a* and *d*, and
'*aa*' '*ad*' and '*dd*' indicate pooled digenic epistatic effects.

Data from unequal number of samples as well as unequal variances among segregating and non-segregating generations were adjusted. To adjust the sample size and variance differences, weighting method by Kearsey and Pooni (2004) using the following equation was applied.

$$\text{Weight } (wt_i) = \text{Generation size } (n_i) / \text{Variances } (S_i^2) \quad (2)$$

Coefficients of genetic components (i.e. additive and dominance and di-genic epistatic effects of additive x additive, additive x dominance and dominance x dominance) suggested by Mather and Jinks (1977) were used in the estimations.

To perform the matrix calculations, a Microsoft Excel® (2007) template was developed. A chi-square test was employed to test the goodness of a model fit. A model was accepted when the three parametric model (i.e. model with *m, a and d*) components showed non-significant differences among the expected and observed genetic component values, otherwise the analysis was performed again with the six parametric model (i.e. model with *m, a daa, ad* and *dd* components). Subsequently, for the six parametric genetic models which showed significant chi-square values, individual genetic components were tested for significance using a t-test. Individual genetic components that showed a significant difference from zero ($p \leq 0.05$) were considered to have contributed to the genetic model.

The simplest model that exhibited non-significant chi-square test result for differences between observed and expected means of every trait, was considered as good and fit.

Estimation of heritability

The genetic variance (V_G) and environmental variance (V_E) were estimated using the within-generation variances of F_2 and non-segregating generations. The following equations were used to estimate narrow-sense heritability (h_N^2) and broad-sense heritability (h_B^2) (Kearsey and Pooni, 2004):

$$h_N^2 = (V_A^*) / (V_A^* + V_D^* + V_E) \quad (3)$$

$$h_B^2 = (V_A^* + V_D^*) / (V_A^* + V_D^* + V_E) \quad (4)$$

where,

$V_A^* = |2V_{F2} - V_{BC1} - V_{BC2}|$

and

$V_D^* = |V_{BC1} + V_{BC2} - V_{F2} - Pooled\ V_E|$

are variances due to additive genetic component effects and dominance genetic component effects, respectively; and $PooledV_E = \frac{SS_{P1} + SS_{P2} + SS_{F1}}{n_{P1} + n_{P2} + n_{F1}}$ is the variance due to environmental effects where *SS* refers to the sum of squares and *n* refers the population size. The * notation in V_A and V_D is to distinguish the special case of equal allele frequencies (Kearsey and Pooni, 2004).

Estimation of mid-parent and better-parent heterosis, and inbreeding depression

Estimates of heterosis based on mid-parent and better-parent values were calculated using the following equations:

$$\text{Mid-parent heterosis} = \frac{\overline{F}_1 - (\frac{\overline{P}_1 + \overline{P}_2}{2})}{(\frac{\overline{P}_1 + \overline{P}_2}{2})} \quad (5)$$

$$\text{Better-parent heterosis} = \frac{\overline{F}_1 - \overline{P}_B}{\overline{P}_B} \quad (6)$$

where $\overline{F}_1$, $\overline{P}_1$, $\overline{P}_2$ and $\overline{P}_B$ were mean values of traits measured on F_1, P_1, and P_2 generations, and better parent, respectively.

Inbreeding depression was estimated using the following equation:

$$\text{Inbreeding depression} = \frac{\overline{F}_1 - \overline{F}_2}{\overline{F}_1} \quad (7)$$

where $\overline{F}_1$ and $\overline{F}_2$ were mean values of F_1 and F_2 generations, respectively.

RESULTS

Mean stalk dry weight and standard deviation values of the various generations in both populations are presented inTable 2. Effects of generations were significant in both populations. Pre-planned LSD test was employed to compare means. Significant differences in stalk dry weight among generations were observed in both populations. As expected, the F_1 generation had the highest stalk dry weight among the generations of Population 1, whereas BC_1P_1 generation revealed the highest stalk dry weight among the generations in population 2.

Results of analysis of generation means for stalk dry weight at maturity in the two populations are presented in Table 3. Non-significant joint-scaling test result for population 1 revealed that the five parametric models was adequate in explaining the genetic control of stalk dry weight, while a three parametric model was adequate for population 2.

Pooled dominance effects were larger than the pooled additive effects in both populations. In the five parametric models in population 1, the largest effect was due to dominance effect, while in the three parametric model in population 2 the largest effect was due to the generations mean effects. The estimate of mean was non-significant in population 1. Additive x dominance [*ad*] epistatic effect was negative in population 1.

Estimates of mid-parental heterosis, inbreeding depression, broad-sense heritability and narrow-sense heritability for stalk dry weight in populations 1 and 2 are shown inTable 4. Estimates of mid-parental heterosis, better-parent heterosis, inbreeding depression, broad-sense heritability and narrow-sense heritability in population 1 were greater than those in population 2. Mid-parental heterosis and better-parent heterosis in population 1 were moderately high, being 54.9 and 9.0%, respectively. High broad-sense and narrow-sense heritability estimates were revealed in population 1, while the estimates were low in population 2.

Bast percentages in generations of population 1 and 2 were almost consistent. Ghana07 (as common parent in both populations) revealed higher bast percentage than 1×51 and Gregg. The F_1 generation in population 2 revealed the highest bast percentage and was the only generation that significantly differed from the other generations in population 2.

Joint-scaling test revealed non-significant differences among observed and expected bast percentage mean values with five- and four-parametric models in populations 1 and 2, respectively. The only adequate model for population 1 was a five parametric model, although pooled dominance and additive x additive epistatic effects were not significantly different from zero. In population 2, results of the joint scaling test revealed that a four parametric model was suitable, although pooled additive effect was not significantly different from zero. Pooled dominance effects were larger than pooled additive effects in both populations.

Mid-parental heterosiswas estimated to be 10.5 and 18.1% in populations 1 and 2, respectively. Estimates of inbreeding depression between the populations also showed relatively large differences with 5.1% in population 1 and 15.4% in population 2. Broad-sense heritability estimates also largely differed between the two populations, with values of 68.
2 and 20.5% for populations 1 and 2, respectively; whereas, narrow-sense heritability estimates in the two populations were close to each other, with values of 13.8 and 10.6% for populations 1 and 2, respectively.

Pre-planned LSD test employed to compare means revealed significant differences in days to flowering among generations in population 1, while no significant differences were observed among generations
in population 2. Ghana07 (as common parent in both populations) revealed a lower mean days to flowering than did 1×51 and Gregg. The F_1 in population 1 had the highest days to flowering (77 days).

Analysis of generation means was not performed on population 2 as no significant differences were revealed among its generations by the LSD test. Analysis of generation means was employed for days to flowering in population 1.

Joint-scaling test revealed non-significant differences among observed and expected mean days to flowering with a four-parametric model in population 1. However, pooled dominance and additive x additive epistatic effects were not significantly different from zero in population 1. Mid-parental heterosis was estimated to be 19.2% for population 1. A very high broad-sense heritability of 99.1% was revealed in population 1.

Effects of generations were significant in population 1, but were non-significant in population 2. Pre-planned LSD test was employed to compare means. LSD test revealed significant differences in plant height among generations in population 1, whereas there were no significant differences among generation means in population 2. 1×51 revealed a larger mean value (269.1 cm) for plant height than did Ghana07 (173.1 cm) in population 1.

Analysis of generation means was not performed on population 2, as there were no significant differences among its generations. Analysis of generation means was employed to study genetic content of plant height in population 1. Joint-scaling test revealed non-significant differences among observed and expected plant height mean values using a five-parametric model, although pooled dominance and dominance x dominance epistatic effects were not significantly different from zero.

Pooled dominance effects were larger than pooled additive effects in both populations. Results of generation means analysis showed that plant height was mainly controlled by pooled additive [*a*] effects and additive x additive [*aa*] epistatic effects.

Mid-parental heterosis, inbreeding depression, broad-sense heritability and narrow-sense heritability were not estimated for plant height in population 2, since there were no significant differences among generations. Small mid-parental heterosis value of 2.5% was revealed for plant height, and inbreeding

depression was estimated to be 10.2%. Broad- and narrow-sense heritability values were estimated to be 74.3 and 53.0%, respectively.

Stalk diameter was measured at the stalk base. Generation effects on basal stalk diameter were significant in population 1, but were not significant in population 2. Pre-planned LSD test employed to compare means showed significant differences in basal stalk diameter among generations in population 1, whereas there were no significant differences among generations in population 2. The F_1 generation in population 1 had the highest basal stalk diameter (16.7 mm), and based on result of the LSD test, this was significantly higher than those of other generations in the population.

Analysis of generation means was not performed on population 2, as differences among generations were not significant. However, analysis of generation means was employed to reveal genetic control of basal stalk diameter in population 1. The joint-scaling test revealed non-significant differences among observed and expected mean values for basal stalk diameter for a six-parametric model. All the genetic parameter estimates were significantly different from zero. Pooled dominance × dominance [*dd*] epistatic effect was the largest among all genetic parameters estimated. Mid-parental heterosis, inbreeding depression, broad-sense heritability and narrow-sense heritability were not estimated for basal stalk diameter in population 2 as there were no significant differences among generations. High mid-parental heterosis (32.5%) was observed for basal stalk diameter, and inbreeding depression was estimated to be 25.9%. Broad- and narrow-sense heritability estimates were 43.7% and 36.0%, respectively.

Pearson's correlation coefficients among stalk dry weight, bast percentage, days to flowering, plant height, and basal stalk diameter from 150 randomly selected individual plants of the F_2 generation in population 1 (1X51 × Ghana07) are presented inTable 5. Stalk dry weight was highly significant (at $p \leq 0.01$) and positively correlated with all other traits.

Bast percentage was also highly and positively correlated with all the other traits, except plant height. As expected, days to flowering was highly significantly correlated with all other traits, except plant height, and showed a positive and significant correlation (at $p \leq 0.05$).

Pearson's correlation coefficients among the studied traits, using data from the 150 randomly selected individual plants of F_2 generation in population 2 (Gregg × Ghana07) are presented inTable 5.

Stalk dry weight was highly and positively correlated with days to flowering, plant height, and basal stalk diameter , while significantly and negatively correlated with bast percentage (at $p \leq 0.05$).

Bast percentage was also highly and positively correlated with days to flowering, and negatively correlated with plant height (significant at $p \leq 0.01$).

Plant height was highly and positively correlated with stalk dry weight, while negatively correlated with bast percentage (at $p \leq 0.01$). Plant height was not correlated with days to flowering. Basal stalk diameter showed highly positive correlations with stalk dry weight, and plant height.

Discussion

A five-parametric model was adequate for explaining stalk dry weight in population 1 while an additive-dominance model was adequate for explaining it in population 2. These findings infer that theories of the analysis of generation means adequately fits population 2, while a more complex situation may be present in population 1. In population 1 the mean was not significantly different from zero, which was not expected. This could be due to the violation of some of generation means analysis assumptions.

The complexity in the genetic model of population 1 could be due to the presence of trigenic or higher order epistasis, or maternal effects. In other words, some of the assumptions of generation means analysis were violated.

Mid-parental heterosis estimated in population 1 was larger than that of population 2. Inbreeding depression, broad-sense heritability and narrow-sense heritability estimates were also largely different in the two populations. This could be because of high differences between the two parents of population 1 (cultivars 1×51 and Ghana07), while smaller differences were observed in population 2. High heritability estimates in population 1 was due to larger additive and dominance variances than the environmental variance.

There was no report of genetic study on bast percentage of kenaf in the literature. Based on the non-significant results of joint-scaling test, five- and four-parametric models were adequately fitted for both populations 1 and 2. There was some ambiguity in the genetic models of both populations. In the five-parametric model in population 1, estimates of pooled additive effects [*d*] and additive x additive epistatic effects [*aa*] were not significantly different from zero, according to the results of the t-test; while in the four-parametric model in population 2, the pooled additive effect [*a*] was not significantly different from zero according to the results of the t-test.

These findings indicate that the models fitted were not fully able to explain the genetics of bast percen

Table1. Mean values for fiber yield and quality characteristics of kenaf cultivars used in the study.

Cultivar	Mean value				
	Bast to core ratio	**Stalk dry yield(kg ha^{-1})**	**Stalk height (cm)**	**Days to flowering**	**Middle stalk diameter (mm)**
Gregg	0.54	10001	262	63	12.9
1X51	0.49	14468	297	84	13.1
Ghana07	0.62	8280	243	75	14.8

Source: Foroughi, 2012.

Table 2. Means and standard deviation (SD) for the traits studied in two kenaf populations.

Studied traits	Families						
	P_1 (♀) N:18	**P_2 (♂) N:18**	**F_1 N:18**	**F_2 N:150**	**BC_1P_1 (F_1♀ x P_1♂) N:50**	**BC_1P_2 (F_1♀ x P_2♂) N:50**	**L.S.D (0.05)**
Stalk dry weight (g)							
Mean (P_1)	34.50	14.10	37.60	21.80	23.20	30.50	5.7
SD (P_1)	6.20	7.25	6.58	8.70	10.08	9.33	
Mean (P_2)	17.70	12.40	18.00	17.40	18.90	16.70	4.4
SD (P_2)	8.51	4.72	6.02	7.62	7.21	7.88	
Bast percentage (%)							
Mean (P_1)	36.70	39.00	41.80	39.60	39.00	37.00	2.1
SD (P_1)	2.83	2.40	1.28	3.42	3.80	3.35	
Mean (P_2)	36.20	37.20	43.40	36.40	37.70	37.10	1.8
SD (P_2)	5.40	3.35	2.60	4.12	4.54	3.95	
days to flowering							
Mean (P_1)	66.70	62.70	77.10	68.50	73.80	65.60	4.3
SD (P_1)	1.28	0.97	0.42	9.98	11.09	6.43	
Mean (P_2)	67.10	64.80	64.70	63.10	66.50	62.20	3.7
SD (P_2)	0.54	3.65	1.28	8.89	7.00	7.47	
plant height (cm)							
Mean (P_1)	269.00	173.00	227.00	204.00	232.00	199.00	16
SD (P_1)	20.87	20.14	20.44	30.60	22.69	22.20	
Mean (P_2)	175.00	166.00	176.00	183.00	192.00	174.00	27
SD (P_2)	24.44	25.74	24.58	21.11	17.73	16.56	
stalk basal dimeter (mm)							
Mean (P_1)	15.10	10.20	16.70	12.40	13.80	12.70	1.4
SD (P_1)	2.11	2.14	1.83	2.49	2.34	2.07	
Mean (P_2)	11.50	10.10	10.00	11.50	11.80	11.20	2.5
SD (P2)	2.64	1.49	1.75	2.50	2.03	2.17	

N = number of samples (single plant); ♀ = female parent; ♂ = male parent; LSD = least significant difference; P_1: (1X51 x Ghana07); P_2: (Gregg x Ghana07).

tage. Some assumptions of the generation means analysis might have been violated.

Moderately high mid- and better-parent heterosis indicates that high bast percentage could be achieved in hybrids through a hybrid breeding strategy. High inbreeding depression indicates that bast percentage decreases significantly in the F_2. Broad-sense heritability in population 1 was considerably higher than that in population 2, while the difference in narrow-sense heritability was not large between the two populations. Therefore, it can be generalized that genetic variance was high in population 1.

Generation mean analysis in population 1 revealed that a four-parametric model adequately explained the genetics of days to flowering. Generation effects were not significant for days to flowering in population 2, and therefore, generation mean analysis was not performed for this trait. The pooled additive effect was significantly different from zero (based on t-test), although pooled dominance and pooled

Table 3. Results of the analysis of generation means for the studied traits.

Studied traits	Genetic parameters estimate						(χ^2) value[§]	p
	M	**[*a*]**	**[*d*]**	**[*aa*]**	**[*ad*]**	**[*dd*]**		
Stalk dry weight (g)								
Value (P_1)	5.87^{ns}	10.22**	31.98**	18.54**	-17.60**	____	0.18^{ns}	0.750 - 0.500
S. E. (P_1)	4.94	1.12	13.49	4.81	4.49	____		
Value (P_2)	15.62**	2.72**	3.23**	____	____	____	1.60^{ns}	0.500-0.250
S. E. (P_2)	0.79	0.8	1.44	____	____	____		
bast percentage (%)								
Value (P1)	37.34**	1.30**	4.46^{ns}	0.53 ^{ns}	-6.45**	____	0.67^{ns}	0.250 - 0.500
S. E. (P1)	1.87	0.44	5.03	1.82	1.68	____		
Value (P2)	30.64**	-1.35^{ns}	12.47**	5.38**	____	____	6.04^{ns}	0.025-0.050
S.E. (P2)	2.3	0.75	6.22	2.17	____	____		
days to flowering								
Value (P1)	59.69**	2.04**	17.37^{ns}	5.00^{ns}	____	____	4.47^{ns}	0.025 - 0.050
S.E. (P1)	4.88	0.19	12.69	4.88	____	____		
plant height (cm)								
Value (P1)	180.76**	48.05**	47.06^{ns}	40.91**	-15.59^{ns}	____	0.34^{ns}	0.500-0.750
S.E. (P1)	13.86	3.42	35.4	13.43	11.28	____		
stalk basal dimeter (mm)								
Value (P1)	15.30**	2.43**	-13.00**	-2.66**	3.32**	14.44**	Ne^{ns}	
S.E. (P1)	1.25	0.35	3.31	1.2	1.13	2.24		

S.E. = Standard error; *m* = mean; [*a*] = pooled additive effects; [*d*] = pooled dominance effects;[*aa*] = pooled additive x additive epistatic effect; [*ad*] = pooled additive x dominance epistatic effect; [*dd*] = pooled dominance x dominance epistatic effect; [§] joint-scaling test χ^2 value; **, [ns]significantly different from zero at $p \leq 0.01$ and non-significant, respectively; which shows non-effective genetic component in the model; P_1: (1X51 x Ghana07); P_2: (Gregg x Ghana07); Ne = negligible value.

Table 4. Mid-parental heterosis, inbreeding depression, broad-sense heritability and narrow-sense heritability estimates for the traits studied.

studied traits	Value (%)				
	Mid-parent heterosis	**Better-parent heterosis**	**Inbreeding depression**	**Broad-sense heritability**	**Narrow-sense heritability**
Stalk dry weight (g)					
P_1	54.9	9.0	42.2	70.3	24.9
P_2	19.9	1.9	3.6	19.3	3.7
Bast percentage (%)					
P_1	10.5	7.2	5.1	68.2	13.8
P_2	18.1	16.6	15.4	20.5	10.6
Days to flowering					
P_1	19.2	15.6	11.1	99.1	35.0
Plant height (cm)					
P_1	2.5	-15.8	10.2	74.3	53.0
Stalk basal dimeter (mm)					
P_1	32.5	11.1	25.9	43.7	36.0

P1: (1X51 x Ghana07); P2: (Gregg x Ghana07).

Table 5. Pearson's correlation coefficients among traits for data obtained from 150 individual plants of F_2 generation in population 1 (P_1) and 2 (P_2).

	Bast %	Days to flowering	Plant height	Basal stalk diameter
P_1				
Stalk dry weight	0.19**	0.20**	0.69**	0.79**
Bast %		0.36**	0.02**	0.21**
Days to flowering			0.12**	0.23**
Plant height				0.66**
P_2				
Stalk dry weight	-0.13**	0.19**	0.46**	0.72**
Bast %		0.17**	-0.19**	-0.08**
Days to flowering			-0.02**	0.05**
Plant height				0.49**

*, ** significant at $p \leq 0.05$ and $p \leq 0.01$, respectively, N = 150.

additive × additive effects included in the model (based on the joint-scaling test) were not significantly different from zero (based on t-test). Significant additive x additive epistasis has been reported by Ketata *et al*. (1976) for heading date in wheat. The non-significant pooled dominance effects and significant pooled additive effects suggest that this trait can be improved effectively by initiating selection in the F_2 generation. Tefera and Peat (1997) reported that a six parametric model was adequate for explaining days to heading and days to maturity in t'ef (*Eragrostistef*) where additive variances were higher than the respective dominance variances.Tefera and Peat (1997) also reported high narrow-sense heritability values for days to heading and days to maturity in that crop.

Tefera and Peat (1997) reported a simple additive-dominance model for the variation in panicle length, culm diameter and plant weight in t'ef (*Eragrostistef*), where the additive variances for plant height and panicle length, were higher than the respective dominance variances. Significant additive, dominance and additive x additive gene effects have been observed for plant height and days to maturity in pearl millet from generation means analysis (Wilson *et al.*, 1990). Plant height is also known to be controlled by epistatic gene action in barley (Thomas and Powell, 1990). A five-parametric genetic model was fitted for plant height in population 1 based on joint-scaling test, while a six-parametric model was found to be adequate for basal stalk diameter in population 1. These findings showed that both traits have a complex genetic make-up, where epistatic effects play a significant role in the genetic control of the traits.

Moderately high broad- and narrow-sense heritability values were estimated for plant height and basal stalk diameter. Tefera and Peat (1997) also reported high narrow-sense heritability values for plant height, panicle length, days to heading and days to maturity. Pooled additive effects for both traits were also significantly different from zero according to the result of the t-test. Therefore, it can be generalized that the traits could be improved through selection of superior individual plants in segregating generations.

Correlations of fiber yield and quality with other traits are important in kenaf breeding programs. Pearson's phenotypic correlation coefficients among all traits measured were generally high in both populations.

As expected, stalk dry weight showed a highly significant and positive correlation with plant height, and basal stalk diameters in both populations. These findings suggest effective applicability of indirect selection for fiber yield using the correlated traits.

Bast percentage was positively correlated (at $p \leq 0.01$) with stalk dry weight in population 1. However, it was negatively correlated (at $p \leq 0.05$) with stalk dry weight in population 2. This inconsistency in correlation of bast percentage with yield may give rise to difficulties in conducting selection programs for fiber yield and quality. Results on correlations found in this study were in agreement with the findings of Foroughi (2012).

The genetic study on stalk dry weight in populations revealed that the high pooled additive effects and the large broad- and narrow-sense heritability could be exploited for successful selection of superior individual plants in segregating generations of population 1. In population 2, pooled additive and dominance effects were significantly different from zero. However, the low broad- and narrow-sense heritability estimates showed that selection for the trait in population 2 will not lead to a significant improvement.

High bast percentage in the stalk implies high fiber quality of the whole stalk. However, generation means analysis results were not consistent in the two populations. In population 1, pooled additive effects were significant, while pooled dominance effect was non significant. The opposite was true in population 2. However, moderately high heterosis estimates in both populations suggests that bast percentage could be improved through hybrid breeding.

Plant height and basal stalk diameter were both mainly controlled by pooled additive and additive × additive effects. Their broad- and narrow-sense heritability values were moderately high indicating that these traits could be improved by selection in segregating generations. Since plant height and basal stalk diameter were highly correlated with stalk dry weight and were moderately heritable, it can be concluded that stalk dry weight can be indirectly improved by the selection of tall plants with a high stalk diameter.

Kenaf is an important industrial crop and considered as a renewable source for the bio-composite industry. However, available information on kenaf genetics is very limited, thus causing it to remain on the verge of commercialization. This study revealed important information on the genetics of kenaf.

Analysis of generation means revealed that bast percentage was mainly controlled by dominance effects whereas stalk dry weight was mainly controlled by additive effects. Estimates of heterosis based on mid-parental values were generally high and ranged from 10 to 55% for stalk dry weight and bast percentage. In general, because of high estimates of high-parent heterosis over mid-parent heterosis, it can be concluded that over dominance effects were present instead of partial dominance. High over dominance effects indicate the usefulness of developing inbred lines selected for high combining ability for hybrid cultivar production. Estimates of inbreeding depression, calculated from F_1 and F_2 generation means, were 55% for stalk dry weight in population 1 (i.e. derived from 1X51 x Ghana07 cross) and 1.43% for population 2 (i.e. derived from the Gregg x Ghana07 cross). Estimates of inbreeding depression for bast percentage were 5% for population 1 and 15% for population 2. The genetic study on stalk dry weight in the populations revealed that the high pooled additive effects and the large broad- and narrow-sense heritability values could be exploited for successful selection of superior individual plants in segregating generations of population 1. In population 2, pooled additive and dominance effects were significantly different from zero. However, the small broad- and narrow-sense heritability estimates showed that selection for the trait in population 2 will not lead to significant improvement.

In conclusion, the portion of phenotypic variations, which is controlled by additive effects, was generally high for stalk dry weight. Thus, selection in the segregating generations would lead to significant improvement in fiber yield.

Classical genetic study (generation means analysis) revealed important information which leads to better understanding of genetic makeup of important traits of kenaf.

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