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RESEARCH ARTICLE

Combining ability and heterosis analyses for oil and healthy fatty acid composition in groundnut (*Arachis hypogaea* L.)

Md. Rayhan Sikder[1,2], Md. Abul Kalam Azad[2], Sariful Haque Bhuiya[2], Khondakar Sumsul Arefin[2], Md. Mahbubul Hasan Shohag[2] & Mohammad Anwar Hossain[1*]

[1]Department of Genetics and Plant Breeding, Bangladesh Agricultural University, Mymensingh-2202, Bangladesh
[2]Bangladesh Institute of Nuclear Agriculture, Mymensingh, Bangladesh
Email: anwargpb@bau.edu.bd

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ABSTRACT

Development of a variety having high oil content and desirable fatty acid compositions is a major objective of groundnut (*Arachis hypogaea* L.) breeding programmes. To study the gene action (through combining ability) and heterosis for oil and fatty acids, an experiment was conducted using a 4 × 4 full diallel method. Four parents and their 12 F_1 hybrids were evaluated following a randomized complete block design. Data were recorded for oil, fatty acids and oleic-linolenic (O/L) acid ratio. Highly significant genotypic variation was found among the parents and their F_1 hybrids for the studied traits. The combining ability studies (general, specific and reciprocal) reflected that the oil and fatty acid traits were controlled by both non-additive and additive genes having significant maternal effects. Results also revealed that the parent China Badam was the best general combiner for oil, linolenic acid and O/L ratio whereas the parent Binachinabadam-4 for oleic and linoleic acids. Best SCA performance was found from the cross Dacca-1 × China Badam and Binachinabadam-4 × China Badam for oil, oleic- and linolenic-acid contents. Significant heterosis for oil content was observed in F_1 hybrids obtained from the cross Binachinabadam-4 × China Badam and its reciprocal cross. The cross China Badam × GC (24)-1-1-1 showed a higher O/L ratio (>4) along with lower level of saturated fatty acids. Therefore, these crosses could be exploited in future breeding programmes to develop new lines for higher oil and healthy fatty acid compositions.

Introduction

Groundnut (*Arachis hypogaea* L.), an important oilseed crop in the world, is considered as an important sources of oil, fatty acids, folate, protein and antioxidants (1–3). It is grown in more than 100 countries with a global production of 42.4 Mt from 25.7 Mha of land (2). Groundnut is ranked 4th among the oilseed crops in the world after soybean, rapeseed, and cotton. About 2/3 of the world's total groundnut production is used to produce oil and the remaining 1/3 is used in food products (4). It is the third most important oil seed crop after mustard and sesame in Bangladesh (5). There is a huge shortage in edible oils as Bangladesh requires two Mt of edible oil annually and almost 90% of the consumption is currently imported. Therefore, consumers and related industries have a growing interest in groundnuts for quality oils and food products.

Groundnut seeds commonly contain 40-50% edible oil which varies depending on variety, season, and maturity (6). According to one report (7), groundnut processer's benefit can be increased by 7% through 1% increase in the seed oil content, indicating greater impact of oil content trait for farmers and traders. Groundnut oil is considered as stable and nutritive as it contains right proportions of saturated and unsaturated fatty acids (also known as healthy fatty acids). Oleic acid, a monounsaturated fatty acid, and linoleic acid, a polyunsaturated fatty acid both retain 75 to 80% of the total fatty acids in the groundnut oil. A statistical ratio of oleic and linoleic (O/L) acid in groundnut oil, which ranges from 0.75 to 5.5 or >2 imparts stability and improves its shelf life by delaying the development of rancidity (8) that also indicates the oil quality. Saturated fatty acids increases cholesterol in blood and are thus related to heart problems in human. Whereas unsaturated fatty acids are controls cholesterol levels by reducing low-density lipoproteins (LDL) and by maintaining high-density lipoprotein (HDL), boosts heart health, immune system and anti-cancer potential, lowers

blood pressure, prevents cognitive disorders and increase insulin production (9, 10). With increasing demand of healthy groundnuts, it is imperative to enhance its unsaturated fatty acid contents to increase its acceptance and use.

For improving oil content and quality related traits in groundnut, knowledge of genetic control of these traits regulating oils and fatty acids composition and genetic variation created through hybridization is necessary. Although inheritance of the oil and fatty acid traits has been reported, the mechanism of the inheritance of these traits may be different due to the differences in the parental sources. Previous research on fatty acids in groundnut has been suggested that the inheritance is governed by both additive and non-additive gene actions (11, 12). Diallel crosses and combining ability studies provides an opportunity to know the mode of inheritance and provide a clear concept for breeders to understand the basis on which certain parental traits could be exploited in the breeding programme. Additionally, general combining ability (GCA), specific combining ability (SCA) variance provides breeders an insight on additive and non-additive inheritance, respectively where reciprocal combining ability (RCA) signify the maternal effect (13). Heterosis study also helps the breeder to assess the superiority and inferiority of the F_1 hybrids as compared to their parents and also for selecting suitable parents for achieving higher genetic gain. Considering the above facts, the present research was conducted to know the gene action controlling oil content and fatty acid compositions through combining ability and heterosis analyses that would help the breeder to select parents or superior lines and to set an appropriate breeding program to increase groundnut oil content as well as to improve the oil quality conferring healthy fatty acid compositions.

Materials and Methods

Experimental site and breeding material

The experiment was conducted at the field experimental plot of Bangladesh Institute of Nuclear Agriculture (BINA), Mymensingh, Bangladesh during the period of 2018-2020 using a 4 × 4 intra-specific F_1 diallel cross of groundnut. Breeding material comprised of a set of four groundnut genotypes viz., Binachinabadam-4, Dacca-1, GC (24)-1-1-1 and China Badam, having diverse origin. Phenotype and other details of the parental lines used in the study are mentioned in Table 1 and Fig. 1. All genotypes were

Fig. 1. Phenotypic appearance of four parents **(a)** Binachinabadam-4, **(b)** Dacca-1, **(c)** GC (24)-1-1-1, **(d)** China Badam used in the 4 × 4 full diallel crossing experiment.

Table 1. Groundnut parents used in the study along with different attributes

Varieties/ genotypes	Source	Botanical type	Flowering and maturity date	Plant height	Seed size and shape	100-seed weight (gm)	Oil content %
Binachinabadam-4	Plant Breeding Division, BINA	Spanish	Relatively late	40-60 cm	Small and round	36-42	47
Dacca-1	Plant Breeding Division, BINA	Spanish	Relatively late	40-60 cm	Small and round	36-42	46
GC (24)-1-1-1	Plant Breeding Division, BINA	Valencia	Relatively early	35-50 cm	Medium and elongated	40-50g	48
China Badam	Plant Breeding Division, BINA	Valencia	Relatively early	35-50 cm	Large and elongated	40-50g	49

crossed in complete diallel fashion during the winter of 2018-2019. During 2019-2020, a set of four parents and their 12 F_1 hybrids (6 direct and 6 reciprocal crosses) were evaluated in a randomized complete block design with three replications. Each plot was designed 1.5 m × 5 m in size, consisting of sixteen rows with row length of 1.5 m. Plant to plant and row to row distance were 20 and 30 cm, respectively. All recommended cultural practices and inputs including thinning, hoeing, irrigation and pest control were carried out using the standard procedures.

Determination of oil content

Oil content was determined using Soxhlet method (14) with minor modifications. Two gram of oven dried groundnut seeds of each genotype were weighed and pulverized into fine powder with a mortar and pestle. Then the groundnut meal was extracted with petroleum benzene for 17 hrs in Soxhlet apparatus. Powder weight before and after extraction was taken, the difference between the two weights was expressed in terms of oil percentage. The advantage of using Soxhlet extraction is that the solvent used in this method penetrates faster to the kernel powder, dissolve oil in the solvent and make a complete extraction. Additionally, this method is very efficient, quick, requires less solvent and convenient for automation and is more acceptable than other extraction methods.

Determination of fatty acids

Oil content was analysed for fatty acids through gas chromatography (using a VARIAN, CP-3800 Gas Chromatograph) in Bangladesh Institute of Nuclear Agriculture (BINA), Mymensingh with a flame ionization detector (FID) following the slight modification of the protocol described (15). First, the groundnut oil was converted into fatty acid methyl ester (FAME) which was then injected to the GC machine with FID and different types of peaks with retention time was observed. The observed retention time was compared with the standard FAME (Supelco 37 component FAME mix, CRM47885) to confirm the specific fatty acid presence in the oil.

Data recording and statistical analysis

Data were recorded on oil content (%), unsaturated fatty acid (oleic acid, linoleic, linolenic, palmitoleic acid) and saturated fatty acid (lauric, myristic, palmitic, stearic, arachidic acid) compositions and olic/linoleic acid ratio (O/L). The data were subjected to analysis of variance (ANOVA) valid for RCBD design. ANOVA, mean, combining ability and heterosis were calculated using PB tools version: 1.3 of IRRI (16) and Minitab-17 software. Mean separation was done following Duncan's Multiple Range Test (DMRT) at 5% level of probability. Standard Model 1 was used for combining ability (GCA, SCA and RCA) analysis for each of the trait (17). The amount of heterosis for a particular trait was calculated by comparing the mean of F_1 hybrids over mid-parental value of the traits following standard formula (18).

Results

The results of analysis of variance showed highly significant genotypic differences ($P \leq 0.01$) for oil content and fatty acid compositions among the parents except for oleic/linoleic (O/L) ratio (Table 2).

Oil Content and fatty acid composition in the parents and hybrids

The oil content and fatty acid compositions in the parents and F_1 hybrids of groundnut that were obtained from a 4 × 4 diallel crossing experiment are presented in Table 2. In respect of oil content, the parent Dacca-1 showed the highest percentage of oil content (51.73%) whereas Binachinabadam-4 showed the lowest (47.33%) content of oil (Table 3). The cross combination Binachinabadam-4 × China Badam was the highest oil producer (55.40%) followed by the cross Dacca-1 × China Badam (54.60%) (Table 3). The highest oleic acid was recorded in Binachinabadam-4 (34.60%) whereas the lowest content (21.73%) was recorded in Dacca-1. Among the crosses and reciprocal crosses, GC (24)-1-1-1 × Binachinabadam-4 showed the highest (33.67%) whereas GC (24)-1-1-1 × China Badam showed the lowest (14.90%) oleic acid content. The parent Binachinabadam-4 showed the highest (36.69%) content of linoleic acid. The cross combination Binachinabadam-4 × Dacca-1 showed the highest (28.66%) linoleic acid content whereas the parent Cina Badam and the cross China Badam × GC (24)-1-1-1showed the lowest content (22.14 and 7.11%, respectively) of linolenic acid (Table 3). The highest value (1.54) for O/L ratio was found for the genotype Cina Badam whereas the highest O/L ratio (4.87) was found from the cross China Badam × GC (24)-1-1-1. The highest linolenic acid content (28.05%) was found in the parents GC (24)-1-1-1 whereas the lowest (1.26%) was found in the genotype Binachinabadam-4. Similarly, the highest (47.53%) linolenic acid was found from the cross Dacca-1 × China Badam, however, it showed a non-significant difference with cross China Badam × GC (24)-1-1-1(45.39%). The lowest content of linolenic content was found from the cross GC (24)-1-1-1 × Binachinabadam-4. The cross combination Dacca-1 × Binachinabadam-4 showed the highest (13.59%) palmitoleic acid. Importantly, it's reciprocal cross Binachinabadam-4 × Dacca-1 showed the lowest (3.49%) amount of palmitoleic acid which showed a non-significant difference with the parent Dacca-1 (5.39%) and the cross combination China badam × GC (24)-1-1-1 (6.07%) (Table 3). The parent

Table 2. Analysis of variance for oil content and fatty acid compositions in a 4 × 4 diallel crossing experiment of groundnut

Item	df	Oil (%)	Oleic acid	Linoleic acid	O/L ratio	Linolenic acid	Palmitoleic acid	Lauric acid	Myristic acid	Palmitic acid	Stearic acid	Arachidic acid
Replication	2	0.27	8.47	39.47	1.32	4.91	1.33	1.04	1.95	0.91	2.66	0.94
Genotype	15	18.72**	84.34**	173.71**	3.65	483.68**	11.52**	31.13**	10.44**	24.23**	7.67**	9.17**
Error	30	0.39	8.83	7.62	0.38	5.06	1.68	0.20	0.22	1.91	0.57	0.72

Note: * and ** indicates significant at 5% and 1% level of probability, respectively

Table 3. Oil and fatty acid contents in the parents and F_1 hybrids obtained from a 4×4 diallel crossing experiment of groundnut

Parents	Oil (%)	Oleic acid (%)	Linoleic acid (%)	O/L ratio	Linolenic acid (%)	Palmitoleic acid (%)	Lauric acid (%)	Myristic acid (%)	Palmitic acid (%)	Stearic acid (%)	Arachidic acid (%)
Binachinabadam-4	47.33 hi	34.60 a	36.69 a	0.95 f	1.26 i	9.15 b	0.63 ef	1.48 d	11.59 a	5.26 a	1.64 e
Dacca-1	51.73 de	21.73 d	28.66 b	0.84 f	11.74 h	5.39 de	12.81 a	6.25 a	12.52 a	0.89 fg	1.56 f
GC (24)-1-1-1	49.83 f	28.02 bc	26.40 bc	1.06 d-f	28.05 f	7.93 bd	0.14 f	0.62 efg	7.64 c-f	1.21 e-g	0.35 ij
China Badam	49.00 fg	33.69 a	22.14 c-e	1.54 c-f	21.48 g	6.85 b-d	5.03 b	3.87 c	8.53 b-d	1.35 e-g	0.51 hi
Crosses											
Binachinabadam-4 × Dacca-1	49.30 f	28.88 bc	28.66 b	1.98 f	36.96 de	3.49 e	3.03 d	3.56 c	6.46 c-f	3.71 bc	0.75 gh
Binachinabadam-4×GC (24)-1-1-1	52.30 d	28.36 bc	26.40 bc	1.28 c-f	26.48 f	8.36 bc	1.06 e	1.16 de	8.69 bc	1.87 e-g	1.39 d
Binachinabadam-4×China Badam	55.40 a	27.28 c	23.14 cd	1.26 c-f	28.68 f	7.48 b-d	0.76 ef	0.86 d-g	8.32 b-d	3.13 cd	2.35 c
Dacca-1× Binachinabadam-4	50.96 e	19.96 d	18.68 e-g	1.19 d-f	25.57 f	13.59 a	3.80 c	5.01 b	10.44 ab	3.30 cd	2.16 cd
Dacca-1 ×GC (24)-1-1-1	46.93 i	27.01 c	19.48 d-f	1.41 c-f	35.41 e	8.65 bc	0.77 ef	0.18 g	6.35 d-g	2.11 d-f	2.69 c
Dacca-1 × China Badam	54.60 b	26.92 c	10.90 hi	2.26 c	47. 53 a	8.04 b-d	0.24 f	0.34 fg	5.02 fg	0.68 g	0.41 ij
GC (24)-1-1-1 ×Binachinabadam-4	52.43 bc	33.67 a	23.14 cd	1.58 c-f	21.21 g	7.65 bd	0.70 ef	0.69 d-f	11.17 a	1.73 e-g	1.22 f
GC (24)-1-1-1 × Dacca-1	48.00 gh	27.51 bc	14.44 gh	1.91 c-e	41.48 bc	9.15 b	0.19 f	0.20 g	5.33 fg	2.15 de	2.85 b
GC (24)-1-1-1 ×China Badam	51.46 de	14.90 e	22.23 c-e	0.70 f	39.95 cd	8.27 bc	0.21 f	1.03 d-f	5.53 e-g	4.83 ab	0.86 g
China Badam ×Binachinabadam-4	53.46 b	32.40ab	16.34 fg	2.00 cd	27.56 f	7.10 b-d	1.19 e	1.31 de	12.71 a	2.02 ef	0.25 j
China Badam × Dacca-1	53.63 b	30.68 ac	9.00 i	3.79 b	44.62 ab	6.94 b-d	0.71 ef	0.21 g	5.43 e-g	5.07 a	3.36 a
China Badam ×GC (24)-1-1-1	51.46 de	30.92 ac	7.11 i	4.87 a	45.39 a	6.07 c-e	0.44 ef	1.31 de	4.12 g	5.13 a	0.83 g
Min.	46.80	6.40	4.40	0.40	0.98	3.10	0.10	0.10	3.24	0.16	1.89
Max.	55.70	38.10	39.08	5.11	50.25	14.44	13.76	7.22	14.22	7.56	34.76

Note: Different letters in a column showed significant difference at 5% level of probability following DMRT test

Dacca-1 had the highest percentage of lauric acid (12.81%), myristic acid (6.25%) and palmitic acid (12.52%) while the cross combination Binachinabadam-4 × Dacca-1 showed the highest content of myristic acid and its reciprocal cross (Dacca-1 × Binachinabadam-4) showed the highest content of lauric acid. Similarly, the cross combination China Badam × Binachinabadam-4 had significantly higher percentage of palmitic acid (12.71%) which showed a non-significant difference with the parent Dacca-1, and the cross GC (24)-1-1-1 × Binachinabadam-4 (Table 3). The parent Binachinabadam-4 showed the highest content of stearic and arachidic acid (5.26 and 1.64%, respectively) whereas the cross combinations China Badam × GC (24)-1-1-1 and China Badam × Dacca-1 showed the highest content of stearic acid. The cross combination China Badam × Binachinabadam-4 showed the lowest content (0.25%) of arachidic acid (Table 3).

Analysis of variance for combining ability

The mean squares for GCA, SCA and RCA were highly significant for all traits including O/L ratio (Table 4). The variance due to dominance deviation (V_D) for oils and all fatty acids was much higher than those of the additive deviation (V_A) (Table 4).

Combining ability of parents

The parent China Badam showed the best general combining effect for oil content while the other three parents exhibited negative GCA effects, however, GC (24)-1-1-1 being the poorest (Table 5). Binachinabadam-4 was a good general combiner for oleic, linoleic, palmitic, and stearic acid. In contrast, Dacca-1 was a good general combiner for lauric, myristic and arachidic acid contents. Similarly, GC (24)-1-1-1 was a good combiner for linolenic acid and China Badam for linolenic acid and O/L (Table 5). China Badam was the only parent which showed significant positive GCA for O/L ratio whereas Binachinabadam-4 showed high negative non-significant effect followed by other parental genotypes GC (24)- 1-1-1 and Dacca-1.

For oil content, four cross combinations viz., Binachinabadam-4 × GC (24)-1-1-1, Binachinabadam-4 × China Badam, Dacca-1 × China Badam and GC (24)-1-1-1 × China Badam showed significant positive SCA effects (Table 6). In contrast, different types of fatty acids content mostly showed significant negative to non-significant positive SCA effects. Besides, few cross-combinations showed significant positive SCA effect i.e., Binachinabadam-4 × Dacca-1 for linolenic acid and myristic acid; Binachinabadam-4 × GC (24)-1-1-1 for lauric acid; Dacca-1 × GC (24)-1-1-1 for linolenic and arachidic acid; Dacca-1 × China Badam for linolenic, arachidic acid and O/L ratio and GC (24)-1-1-1 × China Badam for linolenic acid and O/L ratio (Table 6).

Based on the results of RCA effect, the cross combination Dacca-1 × Binachinabadam-4 showed significant positive RCA effects for oleic and linolenic

Table 4. Analysis of variance for combining ability of oils and fatty acid compositions in a 4 × 4 diallel crossing experiment of groundnut

Source of Variation	df	MS										
		Oil	Oleic acid	Linoleic acid	O/L ratio	Linolenic acid	Palmitoleic acid	Lauric acid	Myristic acid	Palmitic acid	Stearic acid	Arachidic acid
GCA	3	6.54**	29.35**	80.11**	1.01**	303.44**	1.70**	21.33**	5.59**	15.64**	1.91**	4.85**
SCA	6	11.41**	22.49**	79.08**	0.08	231.67**	1.41**	15.14**	5.69**	8.66**	4.62**	7.53**
RCA	6	0.42**	33.11**	25.61**	1.36**	19.46**	9.06**	0.12**	0.22**	3.70**	1.68**	1.16**
Error	30	0.13	2.93	2.34	0.12	1.69	0.86	0.06	0.07	0.61	0.14	0.07
V_A		0.09	4.18	3.46	0.12	44.64	0.16	3.67	0.17	3.80	0.21	0.27
V_D		30.10	48.14	188.91	1.67	566.61	1.36	37.11	13.61	19.81	8.24	18.36

Note: * and ** indicates significant at 5% and 1% level of probability, respectively

Table 5. General combining ability effects for oils and fatty acid compositions of parents in a 4×4 diallel crossing experiment of groundnut

Character Parent	Oil (%)	Oleic acid (%)	Linoleic acid (%)	O/L ratio	Linolenic acid (%)	Palmitoleic acid (%)	Lauric acid (%)	Myristic acid (%)	Palmitic acid (%)	Stearic acid (%)	Arachidic acid (%)
Binachinabadam-4	-0.11	2.03**	4.15**	-0.39	-9.08**	0.37	-0.50**	0.18	2.00**	0.62**	0.98
Dacca-1	-0.06	-2.38**	-1.59	-0.02	1.67	-0.11	2.31**	0.99**	-0.10	-0.37	2.98**
GC (24)-1-1-1	-0.91**	-0.57	0.58	-0.06	3.04**	0.29	-1.52**	-0.01	-1.05	-0.31	-1.51*
China Badam	2.10**	0.92	-3.15**	0.46**	4.34**	-0.49**	-0.28	-0.15	-0.84	0.28	-2.46**
SE (gi)	0.14	0.52	0.46	0.11	0.40	0.10	0.08	0.08	0.24	0.12	0.27

Note: * and ** indicates significant at 5% and 1% level of probability, respectively

acid, GC (24)-1-1-1 × Binachinabadam-4 for arachidic acid, China Badam × Binachinabadam-4 for oil content and archidic acid, China Badam × GC (24)-1-1-1 for linoleic and O/L ratio (Table 7). Rest of the traits showed non-significant positive or non-significant negative or significant negative RCA effects in every cross-combination (Table 7).

Heterosis for oil and fatty acids content

For oil content, most of the crosses showed significant positive mid-parent heterosis however the highest significant positive heterosis (15.04%) was found from the cross Binachinabadam-4 × China Badam and the highest significant negative (-7.58%) heterosis was found in the cross combination Dacca-1 × GC (24)-1-1-1 (Table 8). The cross combination GC (24)-1-1-1 × Binachinabadam-4 showed the highest (61.31%) significant positive heterosis for oleic acid however the same cross showed a non-significant positive heterosis (10.05%) for linoleic acid content. In case of O/L ratio, most of the crosses showed non-significant positive heterosis whereas the cross combination China Badam × GC (24)-1-1-1 showed the highest significant positive heterosis (25.64%) followed by the cross combination China Badam × Dacca-1 and its reciprocal cross Dacca-1 × China Badam. In addition, the cross combination Binachinabadam-4 × Dacca-1 showed the highest significant positive (468.43%) heterosis for linolenic acid and the cross combination GC (24)-1-1-1 × China Badam showed the minimum significant positive heterosis (61.30%). In case of plamitoleic acid, the cross combination Dacca-1 × Binachinabadam-4 showed the highest significant positive heterosis (81.59%). Similarly, the cross combination Binachinabadam-4× Dacca-1 showed significant positive heterosis for lauric, myristic and palmitic acid (323.61, 65.93 and 35.63%, respectively). Additionally, the cross combination China Badam × GC (24)-1-1-1 showed the highest significant positive mid-parent heterosis for stearic and arachidic acid (299.48 and 134.34%, respectively) (Table 8).

Discussion

The knowledge on combining ability and type of gene action responsible for the regulation of expression of different traits is important for planning appropriate breeding strategies. Diallel cross has been extensively used for analyses of GCA, SCA, RCA and heterosis. In this research, an attempt has been made to explore the combining abilities of oil and fatty acids content in a 4 × 4 full diallel crosses of groundnut. A significant variation was found for oil content as well as fatty acid compositions among the parents and their hybrids. Similar to our results, significant genotypic differences among parents and their F_1

Table 6. Specific combining ability effects for oils and fatty acid compositions of cross combinations in a 4×4 diallel crossing experiment of groundnut

Character X Crosses	Oil (%)	Oleic acid (%)	Linoleic acid (%)	O/L ratio	Linolenic acid (%)	Palmitoleic acid (%)	Lauric acid (%)	Myristic acid (%)	Palmitic acid (%)	Stearic acid (%)	Arachidic Acid (%)
Binachinabadam-4 × Dacca-1	-0.78*	-3.33**	-5.65**	0.21	8.47**	0.41	-0.38	1.33**	-1.56	0.54	-0.41**
Binachinabadam-4 ×GC (24)-1-1-1	2.10**	1.68	-1.60	0.04	-0.31	-0.63	0.94**	0.01	0.89	-1.25**	0.16
Binachinabadam-4 ×China Badam	2.26**	-1.00	-1.51	-0.22	2.62	-0.25	-0.22	-0.70**	1.23	-0.82**	0.29
Dacca-1 × GC (24)-1-1-1	-3.53**	2.34	-1.65	-0.04	3.52**	0.89	-2.29**	-1.53**	-1.11	0.04	0.93**
Dacca-1 × China Badam	1.10**	2.37	-4.93**	0.79*	9.82**	0.74	-3.53**	-2.31**	-1.94**	0.54	0.39*
GC (24)-1-1-1×China Badam	1.10**	-5.32**	-2.38	0.60*	5.04**	-1.22**	0.15	0.60	-1.39	1.26**	-0.23
SE (sij)	0.20	0.94	0.83	0.19	0.72	0.26	0.14	0.15	0.44	0.24	0.04

Note: *and ** indicates significant at 5% and 1% level of probability, respectively

Table 7. Reciprocal combining ability effects for oil and fatty acid compositions of cross combinations in a 4×4 diallel crossing experiment of groundnut

Character x Crosses	Oil (%)	Oleic acid (%)	Linoleic acid (%)	O/L ratio	Linolenic acid (%)	Palmitoleic acid (%)	Lauric acid (%)	Myristic acid (%)	Palmitic acid (%)	Stearic acid (%)	Arachidic acid(%)
Dacca-1×Binachinabadam-4	-0.91*	4.24**	-2.15	0.40	5.70**	-4.55**	-0.39	-0.73**	-1.99**	0.20	-7.05***
GC (24)-1-1-1 ×Binachinabadam-4	-0.07	-2.65	0.39	-0.09	2.63	-0.31	0.20	0.23	-1.23	0.11	3.63*
China Badam ×Binachinabadam-4	1.14**	-2.56	2.77	-0.25	0.56	0.53	-0.22	-0.23	-2.20**	0.65	7.33**
GC (24)-1-1-1×Dacca-1	-0.43	-0.25	2.52	-0.37	-3.03**	0.08	0.29	-0.01	0.51	-0.23	-2.92
China Badam ×Dacca-1	0.23	-1.88	0.94	-0.43	1.46	0.72	-0.23	0.06	-0.21	-2.20**	-14.42**
China Badam ×GC (24)-1-1-1	0.12	-8.01**	7.55**	2.08**	-2.72	1.26	-0.12	-0.15	0.71	-0.25	-0.28
SE (rij)	0.22	0.78	1.08	0.25	0.92	0.53	0.18	0.19	0.55	0.31	0.62

Note: * and **represent indicates significant at 5% and 1% level of probability, respectively

Table 8. Percentage of heterosis for oil content and fatty acid compositions obtained from a 4 × 4 diallel crossing experiment of groundnut

Character x Crosses	Oil (%)	Oleic acid	Linoleic acid	O/L ratio	Linolenic acid	Palmitoleic acid	Lauric acid	Myristic acid	Palmitic acid	Stearic acid	Arachidic acid
Binachinabadam-4 × Dacca-1	-1.42	0.96	-55.97*	2.52	468.43**	-49.57*	-54.91*	-8.53	-46.36*	23.79	8.76
Binachinabadam-4 ×GC (24)-1-1-1	7.65**	35.89*	6.31	0.15	171.04**	28.54	323.61**	65.93*	35.63*	-13.27	46.43**
Binachinabadam-4 × China Badam	15.04**	-20.09	-25.59	0.05	152.17**	2.16	-73.07*	-67.77*	-17.31	0.15	65.87**
Dacca-1 × Binachinabadam-4	3.89	-29.13*	-42.83*	0.21	293.23**	81.59**	-43.46*	29.57*	-13.35	7.78	-9.26
Dacca-1 × GC (24)-1-1-1	-7.58**	8.59	-29.25	1.95	77.96*	29.86	-88.11**	-94.57**	-36.95*	107.6**	11.54
Dacca-1 × China Badam	7.99**	-2.87	-57.09*	4.13*	186.08**	44.63*	-97.31*	-93.22**	-52.27*	-39.64	86.46**
GC (24)-1-1-1 × Binachinabadam-4	7.92**	61.31**	10.05	0.41	117.14*	40.00*	170.39**	-0.63	74.20**	-19.91	-23.65
GC (24)-1-1-1 × Dacca-1	-5.48*	10.60	-47.55*	1.96	108.44**	27.41	-97.07**	-93.99**	-47.13*	104.42**	11.54
GC (24)-1-1-1 × China Badam	4.14*	-51.71**	-8.40	0.72	61.30*	17.17	-91.75*	-54.07*	-31.57	275.88**	9.56
China Badam × Binachinabadam-4	11.00**	-5.11	-44.45*	1.15	142.38**	-12.17	-57.91*	-50.84*	26.39	-38.90*	-56.45**
China Badam × Dacca-1	8.48**	10.70	-69.96**	10.48**	168.55**	19.94	-91.97*	-95.72*	-48.38*	387.30**	35.65*
China Badam × GC (24)-1-1-1	4.14*	0.22	-70.68**	25.64**	83.25*	-18.63	-82.73*	-41.19*	-49.05*	299.48**	134.34**

* and **indicates significant at 5% and 1% level of probability, respectively

hybrids for oil content as well as fatty acid contents have been reported when the introduced germplasm were crossed in diallel mating scheme (19, 20). In several other studies, highly significant differences for fatty acid profiles (oleic, linoleic, O/L ratio, linolenic and palmitoleic, lauric, myristic, stearic, stearic, palmitic, arachidic acid) have also been reported (19, 21, 22).

Oil content in the parents and hybrids

The oil content values of our studied varieties were ranged from 49.00 to 51.73% whereas among the hybrids and reciprocal hybrids the values ranged from 46.93 -55.40% (Table 3). According to the published reports, the oil content values of peanut varieties in different market types were ranged from 42.0 to 53.8% in the Spanish type and 43.0-48.0% in Valencia type varieties (23-25). Therefore, out results goes well in accordance with the results of other researchers. The percent of oil content in groundnut seeds has been shown to vary with the cultivar, market type and the environmental conditions under which the seeds were produced (25, 26). However, the significant variation for oil content in the genotypes probably due to the genetic makeup and place of their origin (25, 27).

Unsaturated fatty acid compositions and oil quality values

In this study, remarkable differences were observed in the unsaturated fatty acids (oleic, linoleic, linolenic and palmitoleic acid) contents among the peanut varieties and their hybrids (Table 3). Similar to our results, significant variation in oleic and linoleic acid in groundnut were also reported by others (19, 28). It was reported that the ratios of oleic acid to linoleic acid (O/L ratio) determine the quality, storability and shelf-life of groundnut and its products (29). Additionally, high oleic acid peanut has longer shelf-life than low-oleic groundnut. In the present experiment, the means O/L ratio of peanut parents and hybrids were ranged from 0.95–4.87. Similar to our results, Gulluoglu et al. (28) were also reported a similar range of O/L ratio however the fatty acids content in groundnut oil is affected by variety, seasonal variation, genotype, location, air and soil moisture, soil nutrient, planting date, moisture availability, growing condition and maturity (19, 28, 29).

Saturated fatty acids composition

Palmitic and stearic acids are the major saturated fatty acids in groundnut oil however the other saturated fatty acids like lauric, myristic and

arachidic acids are also present smaller quantities (25). In the present study, plamitic and stearic acid were ranges from 7.64-12.52% and 0.89-5.26%, respectively (Table 3). Our results are in agreement with the results of other researchers who reported that the palmitic acid content of peanut cultivars was varied between 8.6-14.1% and stearic acid between 1.6-3.7% (24, 29-32). Recently, it was reported that palmitic and stearic acids percentage values of the peanut varieties were varied between 10.04-12.68% and 2.32- 3.36%, respectively (25). Significant differences for palmitic and stearic acids percentage among the cultivars are attributable to the genetic makeup and place of their origin (27). Additionally, saturated fatty acid compositions in groundnut oil are strongly influenced by genotype, growing season and harvesting time (24, 26).

Combining ability analysis for oil content and fatty acids composition

The variance for combining ability showed highly significant positive GCA and SCA for oil content and fatty acid compositions which indicates the presence of both additive and non-additive gene action on these traits expression. Beside this, significant RCA effects indicate the influence of maternal effect on the traits. The variances due to dominance deviation (V_D) for oil and all fatty acids contents were much higher than the additive deviation (V_A) suggested predominance of non-additive gene action for the inheritance of these traits (Table 4). The involvement of both additive and non-additive gene action for the trait (oil content) has been reported by others (21, 33, 34). However, few studies reported only additive gene effect in controlling the oil content (19, 22). Additionally, non-additive genetic effects for oil content in *Brassica* have also been reported by others (35, 36). Similar to oil traits, both additive and non-additive gene action for unsaturated fatty acids composition were also reported by others viz., oleic acid (21, 34, 36, 38), linoleic acid (21, 34, 38, 39), linolenic acid (40). In addition, additive and non-additive gene action for unsaturated fatty acids were also reported by others such as myrsitic acid (2); stearic acid (19, 37), palmitic acid (37, 38), and arachidic acid (37). However, only additive gene action for linoleic acid was also reported (19). Research on gene effect of palmitoleic acid in groundnut is unexpectedly rare. In sunflower, reports are on additive gene effect for palmitoleic acid inheritance (41). In contrast to our results of saturated fatty acids, only additive gene effect for saturated fatty acids were also reported such as myristic acid (22), plamitic acid (42, 43) and arachidic acid (43, 44).

Heterosis for oil and fatty acid contents

Among the cross combinations, Binachinabadam-4 × China Badam and its reciprocal cross were showed significantly higher positive mid-parent heterosis for oil content (Table 8) which indicates that both additive and non-additive gene action with significant maternal effect in controlling the trait. Similar to our results, significant positive heterosis oil content in both hybrid and reciprocal hybrids were also reported (45). Significant and non-significant negative heterosis for oil content were also found in the cross Dacca-1 ×GC (24)-1-1-1and its reciprocal cross which is in accordance with the earlier results (46). In case of oleic acid, highly significant positive correction was found in the cross GC (24)-1-1-1 and Binachinabadam-4 and its reciprocals. Importantly, linoleic acid content in most of the crosses and reciprocal crosses showed significant negative heterosis. Similar findings were also reported in mustard (*Brassica juncea* L.) (46). The O/L ratio showed positive heterosis for all of the crosses and their reciprocals whereas the GC (24)-1-1-1× China Badam showed the highest significant positive heterosis. Heterosis for linolenic acid content showed significant positive for all of the crosses whereas the highest mid-parent heterosis was found from the cross Binachinabadam-4 × Dacca-1. A similar positive result for linolenic acid content was also reported by other researchers while studying the diallel cross (47) in mustard. In case of palmitic acid, both positive and negative mid-parent heterosis were found however, the highest positive heterosis was found from the cross Dacca-1 × Binachinabadam-4. Mid-parent heterosis for saturated fatty acids (lauric acid, myristic acid, stearic acid, palmitic acid and arachidic acid) showed both positive and negative values. Importantly, negative heterosis of this traits are desirable and the highest negative heterosis for lauric acid and stearic acid was found from the cross Dacca-1 × China Badam, myristic acid from the cross Dacca-1 × GC (24)-1-1-1, palmitic acid from the cross China Badam × GC (24)-1-1-1, and arachidic acid from the cross China Badam × Binachinabadam-4. Similar negative heterosis for saturated fatty acid was also reported in sunflower (48). Importantly, in most of the cases different cross combination exhibited higher superiority in hybrid, therefore, they can be used in isolating potential lines and to break oil decreasing and low quality barrier in groundnut. Therefore, these superior crosses are also expected to produce transgressive segregants.

Conclusion

In this study, significantly higher GCA for oil content, O/L ratio and linolenic acid was observed in the parent China Badam whereas Binachinabadam-4 showed significantly higher GCA for oleic acid and linoleic acid. So, China Badam and Binachinabadam-4 could be selected as best general combiners for these traits. Best SCA performances were observed from the crosses Dacca-1 × China Badam and Binachinabadam-4 × China Badam for oil, oleic and linolenic acid content. They could be promising combiner for improving oil content and essential fatty acids. Significant heterosis was also observed in these cross combinations for these traits. Additionally, the cross China Badam × GC (24)-1-1-1 showed a higher O/L ratio (>4) along with lower level of saturated fatty acids content. The results of the present study also revealed that both additive and non-additive gene action contributes in controlling the oil and fatty acid traits however predominance of non-additive gene effect was observed along with maternal effects. So, selection in later generation

would be more effective in developing new varieties for higher oil and healthy fatty acid compositions.

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Authors' contributions

MAK Azad conceived the idea and designed the experiment. MR Sikder, SH Bhuiya, KS Arefin, MMH Shohag carried-out the experiment and analyzed the data. MAH and MAK Azad supervised the experimental work. MR Sikder and MAH wrote the initial manuscript. MAK Azad did the proof-reading of the final draft. All authors provided critical feedback and helped to shape of the final manuscript.

Conflict of interests

Authors do not have any conflict of interests to declare.

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