Full Length Research Paper

Types of gene effects governing the inheritance of oleic and linoleic acids in peanut (*Arachis hypogaea* L.)

Nattawut Singkham[1], Sanun Jogloy[1]*, Bhalang Suriharn[1], Thawan Kesmala[1], Prasan Swatsitang[2], Prasit Jaisil[1], Naveen Puppala[3] and Aran Patanothai[1]

[1]Department of Plant Science and Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Khon Kaen, 40002, Thailand.
[2]Department of Biochemistry, Faculty of Science, Khon Kaen University, Khon Kaen, 40002, Thailand.
[3]Agricultural Science Center at Clovis, New Mexico State University, Clovis, New Mexico, 88101, USA.

Oleic and linoleic acids are major fatty acids in peanut determining the quality and shelf-life of peanut products. A better understanding on the inheritance of these characters is an important for high-oleic breeding programs. The objective of this research was to determine the gene actions for oleic acid, linoleic acid, the ratio of oleic to linoleic acids (O/L ratio) and percentage oil (% oil) in peanut. Georgia-02C, SunOleic 97R (high-oleic genotypes) and KKU 1 (low-oleic genotypes) were used as parents to generate P_1, P_2, F_2, F_3, $BC_{11}S$ and $BC_{12}S$. The entries were planted in a randomized complete block design with four replications in the rainy season (2008) and the dry season (2008/2009). Gas liquid chromatography (GLC) was used to analyze fatty acid compositions. The data were used in generation means analysis to understand gene effects. The differences in season, generation and generation × season interactions were significant for oleic acid in the crosses Georgia-02C × KKU 1 and SunOleic 97R × KKU 1. Additive, dominance and epistasis gene effects were significant for oleic acid, linoleic acid, O/L ratio and % oil. Initial selection can be carried out in early segregating population, and final selection in late generations.

Key words: Breeding, gene actions, generation mean analysis, groundnut, oil quality.

INTRODUCTION

Peanut (*Arachis hypogaea* L.) is an important sources of oils and nutrients. Peanut kernels contained 33 to 55% oil and 19 to 31% protein (Asibuo et al., 2008). The major fatty acids in peanut oil are oleic and linoleic acids, which accounted for 80% of total fatty acid (Hammond et al., 1997). Oleic acid had negative correlation with linoleic acid ($r = -0.99$), and positive correlation with percentage oil (% oil) ($r = 0.67$) (Anderson et al., 1998; Dwivedi et al., 1993). Peanut seed quality is determined by the fatty acid compositions. The ratio of oleic to linoleic acids(O/L ratio) and iodine value (IV) are indicators of peanut seed quality and shelf-life (Anderson and Gorbet, 2002). Peanut

genotypes with high O/L ratio and low IV had greater flavor stability and longer shelf-life than normal-oleic peanut (Braddock et al., 1995; Mugendi et al., 1998; O'Keefe et al., 1993). Moreover, consumption of high-oleic peanut is beneficial to health as it can reduce low density lipoprotein (LDL) in human (O'Byrne et al., 1997).

Genetic information in oleic acid is important for improving efficiency of peanut breeding programs. Most studies reported one or two genes with simple inheritance that control the trait. High oleic acid character in a natural mutant peanut was controlled by one or two recessive genes (ol_1 and ol_2) (Moore and Knauft, 1989). Possible genotypes for genes controlling oleic acid in Virginia-type peanuts would be $Ol_1Ol_1ol_2ol_2$, $ol_1ol_1Ol_2Ol_2$ and $Ol_1Ol_1Ol_2Ol_2$ (Isleib et al., 1996). The genotypes of low-intermediate O/L Spanish peanut were $Ol_1Ol_1ol_2ol_2$ or $ol_1ol_1Ol_2Ol_2$ (López et al., 2001).

However, quantitative inheritance has been reported also for oleic acid in peanut. Gene actions for oleic acid in

*Corresponding author. E-mail: sanun@kku.ac.th. Tel: +66 43 364 367. Fax: +66 43 364 367.

Abbreviations: O/L ratio, The ratio of oleic to linoleic acids.

peanut were partial dominance, additive and additive $\times$ additive epistasis (Isleib et al., 2006; Mercer et al., 1990; Singkham et al., 2011; Upadhyaya and Nigam, 1999). Moreover, Isleib et al. (2006) reported that high oleic in peanut is not completely recessive gene, and *ol* gene exhibited pleiotropism that influences oleic and linoleic acids. In addition, modifiers and additional epistatic interactions are also important for oleic acid in peanut (López et al., 2001). Generation mean analysis for oleic acid, linoleic acid, O/L ratio and IV showed that additive gene actions played role in these traits (Aruna and Nigam, 2009). In addition, high heritability for oleic acid was reported by Singkham et al. (2010).

However, previous research used low-intermediate oleic peanuts (37 to 53% oleic acid) (Aruna and Nigam, 2009) as the parent to generate the population for genetic study for oleic acid in peanut. Hence, this research selected high-oleic peanuts (80% oleic acid) to generate population for determining the gene actions for oleic acid character. The theory underlying the investigation is that qualitative and quantitative genes governing the inheritance of oleic and linoleic acids, and, therefore, pyramiding genes controlling the two types of inheritance in single peanut genotypes may be possible. The answer to this question is to study generation means of the crosses involving the normal parents and the mutant parent for oleic acid, and this information is not available in the literature. The objective of this study was to determine the magnitudes of different types of gene effects for oleic acid, linoleic acid, O/L ratio and % oil in two peanut crosses with high and low-oleic genotypes. Information obtained will be useful for appropriate breeding strategies for the improvement of this character.

MATERIALS AND METHODS

Plant materials

Three peanut genotypes, namely SunOleic 97R, Georgia-02C and KKU 1, were selected as parents. SunOleic 97R and Georgia-02C had high oleic acid (80%) (Gorbet and Knauft, 2000; Branch, 2003). KKU 1 is currently grown in Thailand and low oleic acid (47%) (Singkham et al., 2010). These parents produced two F_1 crosses during June to October, 2007 including Georgia-02C $\times$ KKU 1 and SunOleic 97R $\times$ KKU 1. The F_1 seeds of each cross were self-pollinated to generate the F_2 generation and backcrossed to both parents to generated backcrosses to the female parent (BC_{11}) and to the male parent (BC_{12}) generations, which was done during November, 2007 to March, 2008.

Field management

The seeds of each cross in the F_2, BC_{11} and BC_{12} generations and their parents were used in the experiment. The entries were planted in a randomized complete block design with four replications for two seasons: the rainy season (June to October, 2008) and the dry season (November, 2008 to March, 2009) at the Field Crop Research Station of Khon Kaen University (KKU) in Northeast of Thailand (16°26′N, 102°50′E, 190 masl). The plots had three rows of 1 m for the two parents and four rows of 1 m for F_2, BC_{11} and BC_{12} generations each

with 50 cm between rows and 20 cm between plants. The cultivar Kalasin 2 was used for border plants, which was planted at the end of a row.

The soil was ploughed three times, and lime at the rate of 625 kg ha^{-1} was incorporated into the soil during soil preparation. Captan (3a, 4, 7, 7a-tetrahydro-2-[(trichloromethyl)thio]-1*H*-isoindole-1, 3(2*H*)-dione) was used to treat the seeds at the rate of 5 g kg^{-1} of seeds before planting to prevent stem rot caused by *Aspergillus niger*, and also treated with 48% ethrel (2-chloroethylphosphonic acid) at the rate of 2 ml l^{-1} water to break seed dormancy. Pre-emergence herbicide, Alachlor (2-cholro-2′, 6′-diethyl-*N*-(methoxymethyl) acetanilide 48% w v^{-1} EC), was applied just after planting at the rate of 3.75 l ha^{-1}.

A seed was planted for each hill. Chemical fertilizers of N-P-K at the rates of 23.4, 10.2 and 19.4 kg ha^{-1} for N, P and K, respectively were applied at 14 days after emergence (DAE). Gypsum (CaSO$_4$) was applied at 45 DAE at the rate of 312 kg ha^{-1}. Carbofuran (2, 3-dihydro-2, 2-dimethylbenzofuran-7-ylmethylcabamate 3% granular) was applied during the early pod forming stage to control subterranean ants (*Dorylus orientalis*). Manual weeding was done to keep the experimental plots free from weeds. The controls of diseases and pests were done during 15 to 70 DAE by weekly applications of carbosulfan [2-3-dihydro-2, 2-dimethylbenzofuran-7-yl (dibutylaminothio) methylcarbamate 20% w v^{-1}, water soluble concentrate] at the rate of 2.5 l ha^{-1}, methomyl [*S*-methyl-*N*-((methylcarbamoyl)oxy) thioacetimidate 40% soluble powder] at the rate of 1.0 kg ha^{-1}. Supplementary irrigation was given during the dry periods in the rainy season with an overhead sprinkler system, and every week in the dry season. The crop was harvest at maturity (R8) (Boote, 1982). Seeds from each plot were bulked and prepared for fatty acid analysis.

Fatty acid analysis

For each entry, 50 mature kernels were bulked as a single sample, and then % oil and fatty acid compositions were determined. The seed sample was ground, and then dried at 70°C for 15 to 20 h. The moisture content of dried sample was measured by weight difference. A dried seed sample of 2 g was used for oil extraction by the Soxtec extractor (50 ml of petroleum ether was used as a solvent).

The extracted oil was determined for fatty acid content by gas liquid chromatography (GLC). The protocol of fatty acid analysis was modified by Bannon et al. (1982). Fatty acid methyl esters (FAME) was prepared by adding 1 ml of 2.5% H_2SO_4/MeOH in 10 mg of oil sample and 100 µl of 0.01 g ml^{-1} heptadecanoic acid (C17:0) an internal standard. The mixture sample was incubated at 80°C for 2 h. After that 200 µl of 0.9% (w v^{-1}) NaCl and 200 µl heptane were added to the mixture sample. The concentration of each oil sample was 33 µg, which was dissolved in a 1 µl of FAME. The FAME sample (2 µl) was injected to GLC with Flame Ionization Detector (FID) for fatty acid analysis.

Shimadzu Gas Chromatograph GC-14B-CR7A and SGE fort GC capillary column (30 m × 0.25 mm ID BPX70 0.25 µm) was used to analyze fatty acid compositions. The carrier gas was helium at a flow rate of 30 ml min^{-1}. The ignition of the FID used hydrogen and air at the rate of 30 and 300 ml min^{-1}, respectively. Oven temperature was maintained at 130°C for 2 min, and then it was programmed at 5°C min^{-1} to 220°C and held the temperature for 8 min. The temperatures of injector and detector were 250 and 300°C, respectively. The standard fatty acids that were used to identify the fatty acid content in peanut varieties consisted of myristic (C14:0), palmitic (C16:0), stearic (C18:0), oleic (C18:1), linoleic (C18:2), linolenic (C18:3), arachidic (C20:0), eicosenoic (C20:1), behenic (C22:0), erucic (C22:1) and lignoceric acids (C24:0). O/L ratio and % oil (Singkham et al., 2011) were computed as follows:

Table 1. Mean squares for oleic acid, linoleic acid, O/L ratio, and % oil evaluated in two seasons in two crosses.

SOV	DF	Georgia-02C × KKU1				SunOleic 97R × KKU1			
		Oleic acid	Linoleic acid	O/L ratio	% oil	Oleic acid	Linoleic acid	O/L ratio	% oil
Season (S)	1	213.4**	331.8**	3.6	54.4*	27.0	51.0**	0.1	153.4**
Rep/Season	6	1.8	1.5	1.4	9.4	14.4	2.0	4.8	2.6
Generation (G)	5	993.4**	696.4**	453.9**	50.6**	989.2**	512.1**	411.5**	41.4**
G × S	5	41.7**	29.0**	6.0**	26.8**	26.7*	13.7**	1.5	20.4**
Error	30	3.5	2.3	0.9	2.7	9.8	2.3	3.7	4.2
Total	47								
CV (%)		3.1	7.9	16.1	3.5	5.1	8.2	32.9	4.5

Significant at * $p < 0.05$, and ** $p < 0.01$.

O/L ratio = % oleic acid / % linoleic acid,

Percentage of oil   = (oil weight (g) × 100)/ground seed weight (g).

Statistical analysis

Analysis of variance was performed for oleic acid, linoleic acid, O/L ratio and % oil according to a randomized complete block design, and error variances were tested for homogeneity for the two seasons (Gomez and Gomez, 1984). Combined analysis of variance was carried out for all characters. The least significant difference (LSD) was used to compare means differences at 0.05 probability level.

A generation means analysis for each character was performed for each cross to determine additive, dominant, additive × additive, additive × dominance and dominance × dominance effects (Hayman, 1958). Gamble's notations: m, a, d, aa, ad, and dd, were used to describe gene effects, where m = mean, a = sum of additive gene effects, d = sum of dominance gene effects, aa = sum of additive × additive gene effects, ad = sum of additive × dominance gene effects, and dd = sum of dominance × dominance gene effects (Gamble, 1962). The joint scaling test (Cavalli, 1952) was carried out to provide the best estimates of the genetic parameters.

As the various generation means did not have homogeneous variances, they were weighted using the inverse of the variance (Nigam et al., 2001; Suriharn et al., 2005; Simla et al., 2009). The regression analysis was used to find the best fit model (Torres et al., 1993), including the parameters m, a, d, aa, ad and dd, respectively. Any effect that was not significant (5% level of probability) was omitted from the model. Finally, only significant parameters were fitted using the weighted least squares method (Rowe and Alexander, 1980). All calculations for generation means analysis were performed using Microsoft Excel program.

RESULTS

Generations were significantly different for oleic acid, linoleic acid, O/L ratio and % oil in the crosses Georgia-02C × KKU 1 and SunOleic 97R × KKU 1 (Table 1). Most interactions between generation and season were significant for all characters except for the interaction for O/L ratio in the cross SunOleic 97R × KKU 1. Differences between season were significant for oleic acid, linoleic acid and % oil in the cross Georgia-02C × KKU 1 except

for O/L ratio, and significant differences between seasons in the cross SunOleic 97R × KKU 1 were observed for linoleic acid and % oil only.

Generations of the crosses Georgia-02C × KKU 1 and SunOleic 97R × KKU 1 grown in the rainy season and the dry season were significantly different for oleic acid, linoleic acid, O/L ratio and % oil (Table 2). Georgia-02C and SunOleic-97R were consistently higher than KKU 1 for oleic acid, O/L ratio and % oil, but they were consistently lower than KKU 1 for linoleic acid. The means of oleic acid for two crosses in the dry season (2008/2009) were smaller than those in the rainy season (2008). The $BC_{11}S$ generation of the crosses Georgia-02C × KKU 1 and SunOleic 97R × KKU 1 had higher oleic acid than did the $BC_{12}S$ generation in both rainy and dry seasons.

Additive gene actions were consistently significant for oleic acid, linoleic acid and O/L ratio in the crosses Georgia-02C × KKU 1 and SunOleic 97R × KKU 1 in both the rainy season (2008) and the dry season (2008/2009) (Table 3). For % oil, however, additive gene action was significant in the dry season (2008/2009) in the cross SunOleic 97R × KKU 1 only. Dominance gene effects were also consistently significant for oleic acid and linoleic acid. However, the effects were negative and much greater than additive gene effects. Dominance gene effects were not significant for O/L ratio in the cross Georgia-02C × KKU 1 in the dry season (2008/2009). For % oil, dominance effects were significant in the cross SunOleic 97R × KKU 1 in two seasons and Georgia-02C × KKU 1 in the rainy season (2008). All interaction gene effects (additive × additive, additive × dominance, and dominance × dominance) for oleic and linoleic acids were significant for two crosses in the dry season (2008/2009), whereas additive × additive and additive × dominance gene effects for these characters were not significant for the cross Georgia-02C × KKU 1 in the rainy season (2008) (Table 3). Epistasis gene effects were not significant for O/L ratio for the cross Georgia-02C × KKU 1 in the dry season (2008). For % oil, all epistasis effects were significant in the cross Georgia-02C × KKU 1 in

Table 2. Means and standard errors of different generations for oleic acid, linoleic acid, O/L ratio, and % oil in three crosses in the rainy season (2008) and the dry season (2008/2009).

Generation[#]	Oleic acid		Linoleic acid		O/L ratio		% oil	
	Rainy 2008	Dry 2008/2009	Rainy 2008	Dry 2008/2009	Rainy 2008	Dry 2008/2009	Rainy 2008	Dry 2008/0209
	Georgia-02C × KKU1							
P_1	78.0 ± 1.4^a	79.4 ± 0.4^a	3.9 ± 0.5^e	4.0 ± 0.5^d	20.1 ± 2.8^a	22.5 ± 1.6^a	50.8 ± 2.0^a	50.7 ± 0.9^a
P_2	50.0 ± 1.7^e	43.5 ± 1.0^e	26.3 ± 1.5^a	36.7 ± 0.8^a	1.9 ± 0.2^d	1.4 ± 0.1^d	45.1 ± 0.7^{bc}	42.1 ± 1.5^c
F_2	63.0 ± 1.9^c	57.1 ± 2.1^c	16.4 ± 1.0^c	21.6 ± 1.3^c	3.9 ± 0.4^c	2.7 ± 0.3^{bc}	47.4 ± 0.9^b	47.8 ± 1.3^b
F_3	62.1 ± 0.7^c	63.6 ± 3.7^b	17.6 ± 1.2^c	19.8 ± 1.3^c	3.6 ± 0.3^{cd}	3.2 ± 0.2^b	46.8 ± 4.3^b	50.2 ± 1.7^a
$BC_{11}S$	68.2 ± 1.8^b	59.0 ± 1.2^c	11.7 ± 1.6^d	20.2 ± 1.8^c	5.9 ± 1.0^b	3.0 ± 0.3^b	43.7 ± 2.3^c	50.2 ± 1.9^a
$BC_{12}S$	54.7 ± 2.3^d	48.0 ± 0.3^d	23.0 ± 1.4^b	28.1 ± 2.3^b	2.4 ± 0.3^{cd}	1.7 ± 0.1^{cd}	42.4 ± 2.3^c	47.9 ± 0.4^b
MP	64.0	61.5	15.1	20.3	11.0	11.9	48.0	46.4
F-test	**	**	**	**	**	**	**	**
	SunOleic 97R × KKU1							
P_1	79.0 ± 1.7^a	82.4 ± 0.2^a	4.1 ± 0.7^e	4.2 ± 1.2^e	19.8 ± 3.9^a	21.0 ± 5.4^a	45.1 ± 4.0^a	51.0 ± 1.5^a
P_2	49.4 ± 1.9^d	43.6 ± 0.3^d	26.2 ± 1.0^a	30.5 ± 1.5^a	1.9 ± 0.1^b	1.4 ± 0.1^b	40.8 ± 1.2^c	44.4 ± 1.2^{bc}
F_2	64.6 ± 3.2^b	59.4 ± 0.9^{bc}	16.2 ± 1.3^d	20.6 ± 0.4^c	4.0 ± 0.5^b	2.9 ± 0.1^b	45.9 ± 2.1^a	50.0 ± 0.8^a
F_3	63.0 ± 5.9^b	63.5 ± 2.7^b	18.8 ± 0.6^c	16.7 ± 2.6^d	3.4 ± 0.3^b	3.9 ± 0.8^b	41.3 ± 1.4^{bc}	49.0 ± 2.4^a
$BC_{11}S$	61.6 ± 0.5^{bc}	62.2 ± 5.3^b	18.1 ± 0.5^c	20.2 ± 2.9^c	3.4 ± 0.1^b	3.3 ± 0.7^b	44.7 ± 1.7^{ab}	46.2 ± 2.2^b
$BC_{12}S$	58.1 ± 2.3^c	55.5 ± 5.8^c	20.6 ± 2.0^b	24.3 ± 0.4^b	2.9 ± 0.4^b	2.3 ± 0.2^b	44.0 ± 1.4^{abc}	42.7 ± 1.9^c
MP	64.2	63.0	15.2	17.3	10.8	11.2	42.9	47.7
F-test	**	**	**	**	**	**	*	**

[#] P_1, Parental line 1; P_2, parental line 2; F_2, second filial generation; F_3, third filial generation; $BC_{11}S$, first backcross generation with parental line 1 self; $BC_{12}S$, first backcross generation with parental line 2 self; MP, mid-parent value. Significant at * $p < 0.05$, and ** $p < 0.01$. Means in the same column with the same letters are not significantly different by LSD (at $P < 0.05$).

two seasons and the cross Sun Oleic 97R × KKU 1 in the rainy season (2008).

DISCUSSION

The information on the inheritance of oil characters and the gene effects governing the inheritance of the traits is necessary for breeding of peanut for improved oil quality. The question for

the research project is whether generation means analysis could reveal types of gene actions governing the inheritance of oleic acid, linoleic acid, O/L ratio and % oil in peanut as the method has been used expensively in many crops to study many important characters. In peanut, the method was used to study many characters such as peanut bud necrosis disease (PBND) (Pensuk et al., 2004), specific leaf area (SLA), harvest index (HI) (Suriharn et al., 2005) and fatty acids (Aruna

and Nigam, 2009).

For oil characters, Aruna and Nigam (2009) reported that additive and additive × dominance effects controlled oleic acid, linoleic acid and O/L ratio in peanut. Moreover, previous findings showed that additive gene effects were more important than non-additive gene effect for oleic acid in peanut (Mercer et al., 1990; Singkham et al., 2011). Upadhyaya and Nigam (1999) reported that additive × additive epistasis effects were

Table 3. Estimates of different gene effects for oleic acid, linoleic acid, O/L ratio, and % oil in three crosses in the rainy season (2008) and the dry season (2008/2009).

Gene effect[#]	Oleic acid		Linoleic acid		O/L ratio		% oil	
	Rainy 2008	Dry 2008/09	Rainy 2008	Dry 2008/09	Rainy 2008	Dry 2008/09	Rainy 2008	Dry 2008/09
Georgia-02C × KKU1								
m	66.5 ± 0.4**	102.0 ± 6.0**	15.9 ± 0.6**	3.1 ± 1.9**	8.5 ± 2.4**	15.4 ± 1.3**	63.1 ± 1.1**	50.8 ± 0.4**
a	14.0 ± 0.3**	18.0 ± 0.8**	11.2 ± 0.4**	16.4 ± 0.9**	9.1 ± 2.4**	10.5 ± 1.3**	ns	4.3 ± 0.3**
d	-28.4 ± 3.1**	-217.3 ± 36.0**	-12.1 ± 3.7**	-97.1 ± 9.2**	-30.4 ± 15.6**	ns	-99.0 ± 6.2**	ns
aa	ns	-40.5 ± 5.9**	ns	-17.2 ± 1.7**	ns	ns	-15.1 ± 0.9**	-4.4 ± 0.5**
ad	ns	-27.9 ± 12.3**	ns	-33.6 ± 3.7**	-22.2 ± 11.2**	ns	-6.4 ± 1.5**	-8.1 ± 3.9**
dd	42.9 ± 5.1**	254.9 ± 47.9**	22.5 ± 6.4**	120.3 ± 11.3**	42.2 ± 25.0**	ns	135.3 ± 9.1**	-13.1 ± 2.6**
SunOleic 97R × KKU1								
m	76.8 ± 2.2**	76.5 ± 3.5**	13.1 ± 0.6**	4.9 ± 2.7**	11.7 ± 3.5**	15.9 ± 3.2**	30.5 ± 1.9**	65.8 ± 2.0**
a	14.8 ± 0.3**	19.4 ± 3.3**	11.1 ± 0.6**	13.2 ± 0.3**	8.9 ± 3.5**	9.8 ± 3.2**	ns	ns
d	-85.8 ± 13.1**	-69.3 ± 20.6**	-39.7 ± 5.4**	-121.6 ± 16.9**	-51.5 ± 23.6**	-70.2 ± 13.0**	55.1 ± 9.6**	-103.2 ± 9.0**
aa	-12.6 ± 2.2**	-13.4 ± 1.2**	ns	-22.2 ± 2.7**	ns	ns	12.4 ± 1.9**	-18.2 ± 1.9**
ad	-45.2 ± 4.4**	-40.4 ± 13.2**	-34.3 ± 4.7**	-36.3 ± 5.3**	-33.6 ± 19.7**	-35.7 ± 16.4**	-6.1 ± 2.5**	ns
dd	122.8 ± 17.4**	70.3 ± 28.2**	67.0 ± 9.6**	141.2 ± 31.0**	72.2 ± 36.2**	ns	-48.9 ± 11.8**	142.9 ± 11.3**

[#] m, Mean; a, sum of additive effects; d, sum of dominance effects; aa, sum of additive × additive epistatic effects; ad, sum of additive × dominance epistatic effects; dd, sum of dominance × dominance epistatic effects. Significant at ** $p < 0.01$, and ns = non significant.

detected for oleic acid and O/L ratio, and the additive × dominance and dominance × dominance epistasis effects were detected for % oil, and O/L ratio.

The previous results were rather similar to this study in terms of additive gene effects but rather different for dominance gene effects, and epistatis gene effects were predominant for oleic acid, O/L ratio and % oil. The similarity in additive gene actions indicated the importance in quantitative inheritance of the traits in most studies, and the difference in non-additive gene actions between this study and other studies was due to the difference in materials used. In this study, two of the parents were mutants for high oleic, while other studies used normal peanuts.

However, the larger dominance gene effects than additive gene effects for oleic acid, linoleic acid and O/L ratio was due largely to the presence of ol_1 and ol_2 genes in mutant parents (Chu et al., 2009). Moreover, the negative sign of dominance gene effects for oleic acid, linoleic acid and O/L ratio suggested that the effects of dominance genes reduced oleic acid (Rahman and Saad, 2000).

The results supported single gene model and also indicated that recessive gene contributed to high oleic acid. The results also supported multiple genes controlling high oleic. However, the contribution of multiple genes was much smaller than single recessive gene. Therefore, selection for recessive gene should increase oleic acid, and

selection for high oleic and good agronomic traits should be done simultaneously in segregating populations.

In our study, significant seasonal and generation × season interactions were observed for oleic acid. Previous finding reported that seasonal and genotypic × season (environment) interactions were significant for oleic acid in peanut (Anderson and Gorbet, 2002). Moreover, the difference in gene effects between the rainy season (2008) and the dry season (2008/2009) for oleic acid character for the cross Goergia-02C × KKU 1 revealed that the selection for high oleic acid in peanut should determine over seasons. However, the gene effects for oleic acid for the cross SunOleic 97R × KKU 1 were consistent for

both rainy and dry seasons.

In conclusion, additive, the importance of large dominance and epistasis gene effects for oleic acid, linoleic acid and O/L ratio supported non-additive gene controlling the inheritance of these traits.

Therefore, this study supported one gene model. However, the importance of additive gene effect for these traits also suggested the contribution of quantitative inheritance in this peanut population. Selection for segregating high-oleic peanuts should be carried out in early segregating generations, and this practice should reduce affective population size. However, final selection should be carried out in late segregating population in order to fix additive genes.

ACKNOWLEDGEMENTS

REFERENCES

Anderson PC, Gorbet DW (2002). Influence of year and planting date on fatty acid chemistry of high oleic acid and normal peanut genotypes. J. Agric. Food Chem. 50:1298-1305.

Anderson PC, Hill K, Gorbet DW, Brodbeck BV (1998). Fatty acid and amino acid profiles of selected peanut cultivars and breeding lines. J. Food Compos. Anal. 11:100-111.

Aruna R, Nigam SN (2009). Inheritance of fatty acid content and related quality traits in groundnut, *Arachis hypogaea* L. J. Oilseeds Res. 26(1):10-17.

Asibuo JY, Akromah R, Safo-Kantanka O, Adu-Dapaah HK, Ohemeng-Dapaah S, Agyeman A (2008). Chemical composition of groundnut, *Arachis hypogaea* (L) landraces**.** Afr. J. Biotechnol. 7(13):2203-2208.

Bannon CD, Breen GJ, Craske JD, Hai N, Harper NL, O'Rourke KL (1982). Analysis of fatty acid methyl esters with high accuracy and reliability. III. Literature review of an investigation into the development of rapid procedures for the methoxide-catalysed methanolysis of fats and oils. J. Chromatogr. 247:71-89.

Braddock JC, Sims CA, O'Keefe SF (1995). Flavor and oxidative stability of roasted high oleic acid peanut. J. Food Sci. 60:489-493.

Branch WD (2003). Registration of 'Georgia-02C' peanut. Crop Sci. 43:1883-1884.

Boote KJ (1982). Growth stage of peanut (*Arachis hypogaea* L.). Peanut Sci. 9:35-40.

Cavalli LL (1952). An analysis of linkage in quantitative inheritance. In: Reeve ECR, Waddington CH (Eds) Quantitative Inheritance. HMSO, pp. 35-144.

Chu Y, Holbrook CC, Ozias-Akins P (2009). Two alleles of *ahFAD2B* control the high oleic acid trait in cultivated peanut. Crop Sci. 49:2029-2036.

Dwivedi SL, Nigam SN, Jambunathan R, Sahrawat KL, Nagabhushanam GVS, Raghunath K (1993). Effect of genotypes and environments on oil content and oil quality parameters and their correlation in peanut (*Arachis hypogaea.* L.). Peanut Sci. 20:84-89.

Gamble EE (1962). Gene effects in corn (*Zea mays* L.) I. Separation and relative importance of gene effects for yield. Can. J. Plant Sci. 42:339-348.

Gomez KA, Gomez AA (1984). Statistical Procedures for Agricultural Research; John Wiley and Sons: New York.

Gorbet DW, Knauft DA (2000). Registration of 'SunOleic 97R' peanut. Crop Sci. 40:1190-1191.

Hammond EG, Duvick D, Wang T, Dodo H, Pittman RN (1997). Survey of the fatty acid composition of peanut (*Arachis hypogaea*) germplasm and characterization of their epoxy and eicosenoic acids. J. Am. Oil Chem. Soc. 74:1235-1239.

Hayman BI (1958). The separation of epistatic from additive and dominance variation in generation means. J. Hered. 12:371-390.

Isleib TG, Young CT, Knauft DA (1996). Fatty acid genotypes of five Virginia-type peanut cultivars. Crop Sci. 36:556-558.

Isleib TG, Wilson RF, Novitzky WP (2006). Partial dominant, pleiotropism, and epistasis in the inheritance of the high-oleate trait in peanut. Crop Sci. 46:1331-1335.

López Y, Smith OD, Senseman SA, Rooney WL (2001). Genetic factor influencing high oleic acid content in Spanish market-type peanut cultivars. Crop Sci. 41:51-56.

Mercer LC, Wynne JC, Young CT (1990). Inheritance of fatty acid content in peanut oil. Peanut Sci. 17:17-21.

Moore KM, Knauft DA (1989). The inheritance of high oleic acid in peanut. J. Hered. 80:252-253.

Mugendi JB, Sims CA, Gorbet DW, O'Keefe SF (1998). Flavor stability of high-oleic peanut stored at low humidity. J. Am. Oil Chem. Soc. 75:21-25.

Nigam SN, Upadhyaya HD, Chandra S, Nageswara Rao RC, Wright GC, Reddy AGS (2001). Gene effects for specific leaf area and harvest index in three crosses of groundnut (*Arachis hypogaea*). Ann. Appl. Biol. 139:301-306.

O'Byrne DJ, Knauft DA, Shireman RB (1997). Low fat-monounsaturated rich diets containing high-oleic peanuts improve serum lipoprotein profiles. Lipids 32:687-695.

O'Keefe SF, Wiley VA, Knauft DA (1993). Comparison of oxidative stability of high- and normal-oleic peanut oils. J. Am. Oil Chem. Soc. 70:489-492.

Pensuk V, Jogloy S, Wongkaew S, Patanothai A (2004). Generation mean analysis of resistance to peanut bud necrosis caused by peanut bud necrosis tospovirus in peanut. Plant Breed 123:90-94.

Rahman MA, Saad MS (2000). Estimation of additive, dominance and digenic epistatic interaction effects for certain yield characters in *Vigna sesquipedalis* Fruw. Euphytica 114:61-66.

Rowe KE, Alexander WL (1980). Computations for estimating the genetic parameters in joint-scaling tests. Crop Sci. 20:109-110.

Simla S, Lertrat K, Suriharn B (2009). Gene effects of sugar compositions in waxy corn. Asian J. Plant Sci. 8:417-424.

Singkham N, Jogloy S, Kesmala T, Swatsitang P, Jaisil P, Puppala N, Patanothai A (2010). Estimation of heritability by parent-offspring regression for high-oleic acid in peanut. Asian J. Plant Sci. 9(6):358-363.

Singkham N, Jogloy S, Kesmala T, Swatsitang P, Jaisil P, Puppala N, Patanothai A (2011). Combining ability for oleic acid in peanut (*Arachis hypogaea* L.). SABRAO J. Breed. Genet. 43(1):59-72.

Suriharn B, Patanothai A, Jogloy S (2005). Gene effects for specific leaf area and harvest index in peanut (*Arachis hypogaea* L.). Asian J. Plant Sci. 4:667-672.

Torres AM, Moreno MT, Gubero JI (1993). Genetics of six components of autofertility in *Vicia faba*. Plant Breed 110:220-228.

Upadhyaya HD, Nigam SN (1999). Detection of epistasis for protein and oil contents and oil quality parameters in peanut. Crop Sci. 39:115-118.