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# Genotypic Variability and Genotype by Environment Interactions in Oil and Fatty Acids in High, Intermediate, and Low Oleic Acid Peanut Genotypes

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Variability of genotype and genotype × environment (G × E) interactions for fatty acids are important to develop high-oleic types in peanut varietal improvement programs. The objective of this study was to determine the variation in fatty acid composition among peanut genotypes and G × E interactions of fatty acids in three groups of genotypes with high, intermediate, and low-oleic acid. Twenty-one genotypes were tested in three environments consisting of two rainy seasons and one dry season. The results indicated that G × E interactions were significant for biomass, pod yield, and harvest index and also for oleic, linoleic acids, and O/L ratio. G × E interactions were less important than genotypic main effect. For oleic acid, significant interactions were found in the intermediate and low-oleic groups only. Therefore, selection for high-oleic trait in peanut breeding programs should be effective.

**KEYWORDS:** ***Arachis hypogaea*** **L.; fatty acids; high-oleic; genotypic variability; genotype by environment interactions**

## INTRODUCTION

Peanut (*Arachis hypogaea* L.) is an important oil and food crop, containing 42−49% seed oil content (*1*). Oleic (C18:1) and linoleic (C18:2) acid contents account for 80% of total fat. Palmitic acid (C16:0) accounts for another 5−10%, while stearic (C18:0), arachidic (C20:0), eicosenoic (C20:1), behenic (C22:0), and lignoceric acids (C24:0) each account for 1 and 3% of total fat (*2*). The high-oleic peanut lines contain 75.6% oleic (O) and 4.7% linoleic acids (L) compared to 56.1% oleic and 24.2% linoleic acids in normal lines (*3*).

High-oleic acid content and high O/L ratio increase oil quality and shelflife of peanut and its derived products. The high-oleic peanut has longer desirable flavor and shelflife during storage due to a slower decline in roasted flavor and less off-flavor development than normal oleic peanut (*4*, *5*). High-oleic peanut is beneficial to health because it is associated with lowered blood serum cholesterol, especially low density lipoproteins (LDL) in humans (*6*, *7*).

The genetic control of fatty acids is important for improving the peanut quality. Two recessive genes ($ol_1$ and $ol_2$) are known to control the inheritance of high-oleic acid in peanut (*8*). Isleib et al. (*9*) found that four of the normal (low−intermediate) oleic Virginia cultivars have either genotype $ol_1ol_1Ol_2Ol_2$ or $Ol_1Ol_1ol_2ol_2$ and one was $Ol_1Ol_1Ol_2Ol_2$. The low−intermediate oleic acid Spanish peanut cultivars show genotype $ol_1ol_1Ol_2Ol_2$ or $Ol_1Ol_1ol_2ol_2$ (*10*). Therefore, all possible genotypes would be $ol_1ol_1ol_2ol_2$ for high-oleic acid, $ol_1ol_1Ol_2Ol_2$ or $Ol_1Ol_1ol_2ol_2$ for intermediate-oleic acid and $Ol_1Ol_1Ol_2Ol_2$ for low-oleic acid. Previous reports indicated that partial dominance and additive × additive epistasis of the gene controlling was observed for oleic acid traits in peanut (*11*, *12*), then heterozygotes were intermediate-oleic acid.

In addition, Mercer et al. (*13*) found that additive gene effects are more important than nonadditive gene effects in the inheritance for oleic, linoleic, and O/L ratio in peanut. Moreover, López et al. (*10*) found that high-oleic acid in Spanish-type peanut is controlled by two loci, but modifiers and additional epistatic interactions may be occurring. Modifier genes present in different genetic backgrounds may alter the expression of oleic acid leading to genotype (G) × environment (E) interaction. Knowledge of G × E interaction facilitates the efficient use of appropriate breeding and selection procedures.

Seed maturation affects fatty acid compositions in peanut with increased oleic acid, while other fatty acids decreased during maturity (*14*). Percentage of oil in peanut is positively correlated with O/L ratio ($r = 0.60$) and negatively with oleic and linoleic acid content, per se ($r = -0.99$) (*2*, *15*, *16*). Significant genotype, environment, and G × E interactions were observed for oleic, linoleic acid, % oil, and O/L ratio (*16*). Peanut grown under end-of-season drought conditions showed increased oleic acid and decreased linoleic acid with significant G × E interactions for oleic and linoleic acids (*17*). Significant year by planting date interactions were also reported for oleic and linoleic acids (*15*). Variation in soil temperature adversely affects both oleic and linoleic acids (*18*).

The studies conducted so far have worked with peanut genotypes in general, and no attempt has been made to separate groups of

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**Table 1.** Peanut Genotypes Used in the Study

| entry no. | genotype | branching pattern[a] |
|---|---|---|
| | High-Oleic Acid Group | |
| 1 | ANorden | irregular |
| 2 | SunOleic 97R | irregular |
| 3 | Georgia-02C | irregular |
| | Intermediate-Oleic Acid Group | |
| 4 | AT 201 | irregular |
| 5 | KK 60−3 | alternate |
| 6 | KK 6 | alternate |
| 7 | KKU 72−1 | alternate |
| 8 | [(NC17090 × B1)-25 × China97−2]$_{F6-6-2}$ | irregular |
| 9 | [(NC17090 × B1)-9−1 × KK60−3]$_{F6-8-3}$ | irregular |
| 10 | [(NC17090 × B1)-9−1 × KK60−3]$_{F6-8-2}$ | alternate |
| 11 | [(NC17090 × B1)-9−1 × China97−2]$_{F6-14}$ | irregular |
| 12 | [(NC17090 × B1)-25 × KK60−3]$_{F6-7-4}$ | alternate |
| 13 | (Luhua11 × China 97−2)$_{F5-13}$ | sequential |
| | Low-Oleic Acid Group | |
| 14 | Tainan 9 | sequential |
| 15 | KK 5 | sequential |
| 16 | KKU 1 | sequential |
| 17 | KKU 40 | sequential |
| 18 | KK 60−1 | sequential |
| 19 | KK 60−2 | sequential |
| 20 | KK 4 | sequential |
| 21 | Kalasin 2 | sequential |

[a] Descriptors for groundnut.(*25*)

genotypes with different oleic acid content to study G × E interactions in detail. The hypothesis underlying this study is that G × E interactions of oil and fatty acids are different among groups of genotypes with genotypic differences for oleic acid content. The objective of this study was to determine the variation in fatty acids among groups of peanut genotypes and G × E interactions of oil and fatty acids in three groups of genotypes with high, intermediate and low-oleic acid. This information will be useful for peanut breeding aiming at improving seed quality and shelflife through increased oleic acid.

## MATERIALS AND METHODS

**Peanut Genotypes and Crop Management.** Twenty-one genotypes varying in oleic acid content were classified into three groups with high, intermediate, and low oleic acid (**Table 1**). The experiments were carried out in two rainy seasons (2006 and 2007) and one dry season (2006/07) at the Field Crop Research Station of Khon Kaen University (KKU) in Northeast of Thailand (16°26′N, 102°50′E, 190 masl). Each experiment was conducted at a different site. The experiments in the rainy seasons were conducted during June−October, while the dry season experiment was done during December−March. The experiments were conducted in a randomized complete block design with two replications, each. A two-row plot with 5.2 m long and spacing of 50 cm between rows and 20 cm between plants within row was adopted.

Soil preparation was done by ploughing three times. Lime at 625 kg/ha was incorporated into the soil during soil preparation. The seeds were treated with captan (3a,4,7,7a-tetrahydro-2-[(trichloromethyl)thio]-1*H*-isoindole-1,3(2*H*)-dione) at the rate of 5 g/kg of seeds before planting to prevent stem rot (caused by *Aspergillus niger*) and also treated with ethrel (2-chloroethylphosphonic acid) 48% at the rate of 2 mL/L water to break seed dormancy. Three seeds were planted and the seedlings were thinned to obtain two plants per hill at 7 days after emergence (DAE). There were 96 plants in a plot. Chemical fertilizers of N−P−K at 23.4 N kg/ha, 10.2 P kg/ha, and 19.4 K kg/ha were applied at 14 DAE. Gypsum ($CaSO_4$) at the rate of 312 kg/ha was applied at 45 DAE. 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*). Pre-emergence herbicide, Alachlor (2-chloro-2′,6′-diethyl-*N*-(methoxymethyl) acetanilide 48%, w/v, emulsifiable concentrate) at 3.75 L/ha, was applied just after planting. One manual weeding was done to keep the experimental plots free from weeds. During 15−70 DAE, pests and diseases were controlled by weekly applications of carbosulfan [2-3-dihydro-2,2-dimethylbenzofuran-7-yl (dibutylaminothio) methylcarbamate 20% w/v, water-soluble concentrate] at 2.5 L/ha, methomyl [*S*-methyl-*N*-((methylcarbamoyl)oxy) thioacetimidate 40% soluble powder] at 1.0 kg/ha. Supplementary irrigation was given during the dry periods in the rainy season, while the crop was fully irrigated at weekly intervals in the dry season with an overhead sprinkler system.

**Data Collection.** Border plants in each plot were discarded, and the remaining plants were harvested and threshed, and fresh shoot weight was measured. A random shoot sample of 2 kg for each plot was taken, oven-dried at 80 °C for 48 h, and weighed. Shoot dry weight of the sample was then converted to total shoot weight per plot. Pod dry weight was determined after sun drying of the pods to approximately 8% moisture content. Harvest index (HI) is directly related to yield as it represents the proportion of total biomass partitioned into pod.

**Peanut Oil Preparation and Analysis of Fatty Acids.** Fifty mature kernels were used for determination of oil content and fatty acid compositions. Ground seed sample was dried at 70 °C for about 15−20 h. Moisture content was measured by weight difference before and after drying. Two grams of dried ground sample was used for oil extraction by the Soxtec extractor (50 mL of petroleum ether was used as a solvent).

$$\text{percentage of oil} = \frac{\text{oil weight(g)} \times 100}{\text{ground seed weight(g)}}$$

The extracted oil was determined for fatty acid composition by gas liquid chromatography (GLC). The protocol of fatty acid analysis was modified from Bannon (*19*). Fatty acid methyl esters (FAME) were 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 C17:0 an internal standard. The mixture was incubated at 80 °C for 2 h. After incubation, 200 μL of 0.9% (w/v) NaCl, and 200 μL heptane were added to the mixture and mixed well. The FAME was extracted into heptane. The concentration of 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 acids analysis. Fatty acid analysis was conducted on Shimadzu gas chromatograph GC-14B-CR7A and SGE fort GC capillary column (30 m × 0.25 mm ID BPX70 0.25 μm) was used. Helium was the carrier gas at a flow rate of 30 mL/min. Oven temperature was maintained at 130 °C for 2 min. Then it was programmed at 5 °C/min to 220 °C and held at this temperature for 8 min. The injector and detector temperature 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, palmitic, stearic, oleic, linoleic, linolenic, arachidic, eicosenoic, behenic, erucic, and lignoceric acids.

The ratio of oleic (O) to linoleic (L) acid, iodine value (IV), and the ratio of unsaturated to saturated fatty acids (U/S ratio) (*13*) were computed:

$$\text{O/L ratio} = \%\ \text{oleic acid}/\%\ \text{linoleic acid}$$

$$\text{IV} = (\%\ \text{oleic acid} \times 0.8601) + (\%\ \text{linoleic acid} \times 1.7321) + (\%\ \text{eicosenoic acid} \times 0.7854)$$

$$\text{U/S ratio} = (\%\ \text{oleic acid} + \%\ \text{linoleic acid} + \%\ \text{eicosanoic acid})/(\%\ \text{palmitic acid} + \%\ \text{stearic acid} + \%\ \text{arachidic acid} + \%\ \text{behenic acid} + \%\ \text{lignoceric acid})$$

**Statistical Analysis.** Comparisons were made among seasons and peanut genotypes for the fatty acid compositions. A combined analysis of variance was first conducted according to the experiment design, with genotypes as fixed and seasons, random effects (*20*). The sum of squares attributed to genotypes was further partitioned into orthogonal comparisons among three oleic acid groups and among genotypes within each group. The genotype × season interaction sum of squares was also partitioned into the interactions of peanut groups with seasons. The error variances associated with individual comparisons were tested for homogeneity

**Table 2.** Contribution of Sources of Variation for Three Seasons for Fatty Acid Composition Evaluated in Three Environments (Seasons)[a]

| source of variation | df | palmitic acid | stearic acid | oleic acid | linoleic acid | arachidic acid | eicosenoic acid | behenic acid | lignoceric acid |
|---|---|---|---|---|---|---|---|---|---|
| environment (E) | 2 | 0.12** | 0.14** | 0.05** | 0.07** | 0.14 | 0.04** | 0.02 | 0.36** |
| rainy season vs dry season | 1 | 0.06** | 0.14** | 0.04** | 0.06** | 0.13* | 0.04** | 0.00 | 0.19** |
| between rainy seasons 2006 and 2007 | 1 | 0.06** | 0.00 | 0.01** | 0.01** | 0.00 | 0.00 | 0.01 | 0.17** |
| rep within season | 3 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.00 | 0.02 | 0.01 |
| genotypes (G) | 20 | 0.84** | 0.72** | 0.92** | 0.90** | 0.69** | 0.92** | 0.61** | 0.43** |
| among genotype groups | 2 | 0.79** | 0.27** | 0.87** | 0.86** | 0.25** | 0.73** | 0.33** | 0.17** |
| among high-oleic acid genotypes | 2 | 0.00 | 0.00 | 0.00 | 0.0002** | 0.00 | 0.004** | 0.00 | 0.00 |
| among intermediate-oleic acid genotypes | 9 | 0.03** | 0.17** | 0.04** | 0.03** | 0.17** | 0.12** | 0.22** | 0.13** |
| among low-oleic acid genotypes | 7 | 0.01** | 0.28** | 0.02** | 0.01** | 0.27** | 0.07** | 0.06** | 0.13** |
| genotypes × environment (G × E) | 40 | 0.03** | 0.12** | 0.03** | 0.03** | 0.13** | 0.02* | 0.31** | 0.14** |
| among genotype groups × E | 4 | 0.02** | 0.03** | 0.02** | 0.02** | 0.03** | 0.005** | 0.08** | 0.02** |
| among high-oleic acid genotypes × E | 4 | 0.00 | 0.00 | 0.00 | 0.001** | 0.00 | 0.00 | 0.02** | 0.01* |
| among intermediate-oleic acid genotypes × E | 18 | 0.01** | 0.05** | 0.01** | 0.01** | 0.06** | 0.01 | 0.09** | 0.07** |
| among low-oleic acid genotypes × E | 14 | 0.01** | 0.04** | 0.002** | 0.003** | 0.04** | 0.01 | 0.13** | 0.04** |
| pooled error | 60 | 0.01 | 0.02 | 0.00 | 0.00 | 0.02 | 0.02 | 0.04 | 0.05 |
| total | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |

[a] *,** Significant at $p \leq 0.05$ and 0.01 probability levels, respectively. Proportion of sum of squares to total sum of squares.

**Table 3.** Contribution of Sources of Variation for % Oil, the Ratio of Oleic to Linoleic Acid (O/L Ratio), Iodine Value (IV), the Ratio of Unsaturated to Saturated Fatty Acid (U/S Ratio), Biomass, Pod Yield, And Harvest Index (HI) Evaluated in Three Environments (Seasons)[a]

| source of variation | df | % oil | O/L ratio | IV | U/S ratio | biomass | pod yield | HI |
|---|---|---|---|---|---|---|---|---|
| environment (E) | 2 | 0.19 | 0.01* | 0.13** | 0.01 | 0.15** | 0.45** | 0.51** |
| rainy season vs dry season | 1 | 0.03 | 0.01** | 0.12** | 0.00 | 0.15** | 0.13** | 0.03** |
| between rainy seasons 2006 and 2007 | 1 | 0.16 | 0.00 | 0.01** | 0.00 | 0.00 | 0.32** | 0.49** |
| rep within season | 3 | 0.09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| genotypes (G) | 20 | 0.32** | 0.94** | 0.82** | 0.92** | 0.51** | 0.36** | 0.30** |
| among genotype groups | 2 | 0.04** | 0.92** | 0.77** | 0.82** | 0.13** | 0.18** | 0.11** |
| among high-oleic acid genotypes | 2 | 0.01 | 0.01** | 0.002** | 0.003** | 0.01* | 0.01** | 0.01** |
| among intermediate-oleic acid genotypes | 9 | 0.13** | 0.01** | 0.04** | 0.07** | 0.26** | 0.09** | 0.14** |
| among low-oleic acid genotypes | 7 | 0.15** | 0.00 | 0.01** | 0.03** | 0.11** | 0.08** | 0.05** |
| genotypes × environment (G × E) | 40 | 0.26** | 0.04** | 0.05** | 0.06** | 0.30** | 0.18** | 0.15** |
| among genotype groups × E | 4 | 0.00 | 0.01** | 0.03** | 0.03** | 0.09** | 0.01** | 0.01** |
| among high-oleic acid genotypes × E | 4 | 0.03* | 0.03** | 0.002** | 0.002* | 0.01* | 0.01** | 0.01** |
| among intermediate-oleic acid genotypes × E | 18 | 0.15** | 0.00 | 0.01** | 0.02** | 0.17** | 0.10** | 0.08** |
| among low-oleic acid genotypes × E | 14 | 0.07* | 0.00 | 0.01** | 0.00 | 0.03** | 0.05** | 0.05** |
| pooled error | 60 | 0.15 | 0.01 | 0.01 | 0.01 | 0.04 | 0.01 | 0.03 |
| total | | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |

[a] *,** Significant at $p \leq 0.05$ and 0.01 probability levels, respectively. Proportion of sum of squares to total sum of squares.

by Bartlett's test (*20*). The test indicated homogeneity of these variances. The pooled error was used to test significance of genotype × season interaction. Duncan's multiple range test (DMRT) was used to compare mean differences. Combined analysis of variance of three-season data was performed for oil traits, biomass, pod yield, and HI in 21 peanut genotypes. All calculations were done using MSTAT−C package (*21*).

Simple correlation was used to determine the relationship among fatty acid compositions, % oil, O/L ratio, IV, U/S ratio, biomass, pod yield, and harvest index (HI) for three seasons.

## RESULTS AND DISCUSSION

**Soil Properties and Weather Data.** Soil chemical and physical properties were slightly different among experimental sites (data not shown). The soil in the rainy season 2006 trial was much sandier than the soil in the rainy season 2007 trial and dry season 2006/07 because of lower clay particles. Organic matter and nitrogen were higher in the dry season 2006/07 (0.14% of total N) than rainy seasons 2006 and 2007 (0.02 and 0.03% of total N, respectively). The differences in chemical and physical properties can affect the performance of peanut genotypes for fatty acids (*16*).

The average of air temperatures in the rainy seasons of 2006 and 2007 were similar (28.44 ± 1.44 and 27.99 ± 1.73 °C, respectively), which were characterized by closer day and night temperatures and rather stable temperatures across the growth period (data not shown), wherea, the average of air temperatures in the dry season 2006/07 fluctuated more (26.57 ± 3.79 °C), with higher temperatures observed at the end of the growing season (data not shown). The lower temperatures were found in the middle growing season in December 2006 and February 2007. The differences between day and night temperatures in the dry season 2006/07 were wider than those in the rainy seasons of 2006 and 2007. The differences in rainfalls between the rainy and dry seasons might have no significant effects because supplemental irrigation was available for all seasons.

**Genotypic Variability and Genotype × Environment Interactions for Fatty Acids and Agronomic Traits.** Combined analysis of variance showed significant seasonal differences for most characters except for arachidic and behenic acids, % oil and U/S ratio, whereas the genotype and genotype × environment (G × E) were significant difference for all traits (**Tables 2** and **3**). Seasonal differences (rainy vs dry season or between the two rainy seasons) were highly significant for palmitic, oleic, linoleic, and lignoceric acids. Rainy vs dry season also differed for stearic, arachidic, eicosenoic acids as well as O/L ratio. Oleic acid was the highest and linoleic

**Table 4.** Percentage of Fatty Acid Composition, % Oil, the Ratio of Oleic to Linoleic Acid (O/L Ratio), Iodine Value (IV), and the Ratio of Unsaturated to Saturated Fatty Acid (U/S Ratio) for Averaged over 21 Peanut Genotypes[a]

| | fatty acid composition (weight %) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| seasons | palmitic acid | stearic acid | oleic acid | linoleic acid | arachidic acid | eicosenoic acid | behenic acid | lignoceric acid | % oil | O/L ratio | IV | U/S ratio |
| rainy season 2006 | 9.75$^{ab}$ | 4.29$^{a}$ | 59.49$^{b}$ | 20.30$^{b}$ | 1.72 | 1.02$^{b}$ | 2.64 | 1.04$^{ab}$ | 44.19 | 6.06$^{a}$ | 87.11$^{b}$ | 4.32 |
| rainy season 2007 | 8.39$^{b}$ | 4.42$^{a}$ | 63.06$^{a}$ | 17.34$^{c}$ | 1.78 | 1.05$^{b}$ | 2.77 | 1.31$^{a}$ | 46.87 | 6.32$^{a}$ | 85.10$^{b}$ | 4.45 |
| dry season 2006/07 | 10.17$^{a}$ | 3.45$^{b}$ | 55.69$^{c}$ | 24.60$^{a}$ | 1.47 | 1.20$^{a}$ | 2.76 | 0.93$^{b}$ | 46.51 | 4.77$^{b}$ | 91.44$^{a}$ | 4.51 |
| *F* test | **[b] | ** | ** | ** | NS[b] | *[b] | NS | ** | NS | ** | ** | NS |

[a] Means in the same column followed by the same letter (s) are not significantly different (at $p < 0.05$) by DMRT. [b] *, **, and NS significant at $p \leq 0.05$, 0.01, and nonsignificant probability levels, respectively.

**Table 5.** Percentage of Fatty Acid Compositions, % Oil, the Ratio of Oleic to Linoleic Acid (O/L Ratio), Iodine Value (IV), and the Ratio of Unsaturated to Saturated Fatty Acid (U/S Ratio) for 21 Peanut Genotypes Averaged over Three Seasons

| | Fatty acid composition (weight %) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| peanut genotypes | palmitic acid | stearic acid | oleic acid | linoleic acid | arachidic acid | eicosenoic acid | behenic acid | lignoceric acid | % oil | O/L ratio | IV | U/S ratio |
| **High-Oleic Acid Group** | | | | | | | | | | | | |
| ANorden | 6.80$^{hi}$ | 2.43$^{l}$ | 80.02$^{b}$ | 4.15$^{l}$ | 1.17$^{i}$ | 1.90$^{b}$ | 2.45$^{g}$ | 1.20$^{bc}$ | 45.00$^{d-h}$ | 19.38$^{c}$ | 77.50$^{k}$ | 6.15$^{b}$ |
| SunOleic 97R | 6.50$^{i}$ | 2.53$^{kl}$ | 81.32$^{a}$ | 3.60$^{lm}$ | 1.17$^{i}$ | 1.77$^{c}$ | 2.23$^{h}$ | 1.17$^{bcd}$ | 46.92$^{abc}$ | 22.60$^{b}$ | 77.52$^{k}$ | 6.43$^{a}$ |
| Georgia-02C | 6.93$^{h}$ | 2.28$^{l}$ | 80.48$^{ab}$ | 3.28$^{m}$ | 1.15$^{i}$ | 2.03$^{a}$ | 2.25$^{h}$ | 1.27$^{b}$ | 45.43$^{b-g}$ | 24.90$^{a}$ | 76.47$^{k}$ | 6.17$^{b}$ |
| **Intermediate-Oleic Acid Group** | | | | | | | | | | | | |
| AT 201 | 8.12$^{g}$ | 2.82$^{k}$ | 75.20$^{c}$ | 11.30$^{k}$ | 1.28$^{h}$ | 1.53$^{d}$ | 2.37$^{gh}$ | 1.13$^{cde}$ | 48.33$^{a}$ | 6.82$^{d}$ | 85.47$^{i}$ | 5.62$^{c}$ |
| KK 60−3 | 9.52$^{e}$ | 3.52$^{j}$ | 59.95$^{g}$ | 21.35$^{g}$ | 1.50$^{g}$ | 1.03$^{f}$ | 2.70$^{ef}$ | 0.95$^{ghi}$ | 44.90$^{d-h}$ | 2.98$^{fg}$ | 89.37$^{g}$ | 4.53$^{f}$ |
| KK 6 | 7.90$^{g}$ | 5.32$^{b}$ | 62.98$^{ef}$ | 16.87$^{i}$ | 2.07$^{b}$ | 0.98$^{fg}$ | 3.03$^{bc}$ | 1.08$^{def}$ | 45.07$^{c-h}$ | 3.88$^{ef}$ | 84.18$^{j}$ | 4.17$^{g}$ |
| KKU 72−1 | 8.28$^{fg}$ | 4.85$^{c}$ | 63.23$^{e}$ | 16.80$^{i}$ | 2.02$^{b}$ | 1.03$^{f}$ | 2.93$^{cd}$ | 1.07$^{d-g}$ | 42.58$^{i}$ | 3.95$^{ef}$ | 84.27$^{j}$ | 4.23$^{g}$ |
| [(NC17090 × B1)-25 × China97−2]$_{F6-6-2}$ | 8.68$^{f}$ | 4.15$^{e-h}$ | 66.08$^{d}$ | 15.60$^{j}$ | 1.70$^{d}$ | 0.98$^{fg}$ | 2.35$^{gh}$ | 0.80$^{jk}$ | 45.23$^{c-g}$ | 4.40$^{e}$ | 84.63$^{ij}$ | 4.67$^{def}$ |
| [(NC17090 × B1)-9−1 × KK60−3]$_{F6-8-3}$ | 8.68$^{f}$ | 3.93$^{hi}$ | 66.68$^{d}$ | 15.25$^{j}$ | 1.58$^{efg}$ | 0.98$^{fg}$ | 2.27$^{h}$ | 0.78$^{k}$ | 48.38$^{a}$ | 4.58$^{e}$ | 84.52$^{ij}$ | 4.83$^{d}$ |
| [(NC17090 × B1)-9−1 × KK60−3]$_{F6-8-2}$ | 8.53$^{f}$ | 3.72$^{ij}$ | 66.25$^{d}$ | 15.32$^{j}$ | 1.67$^{def}$ | 1.07$^{f}$ | 2.63$^{f}$ | 0.93$^{hi}$ | 46.18$^{b-e}$ | 4.48$^{e}$ | 84.33$^{j}$ | 4.73$^{de}$ |
| [(NC17090 × B1)-9−1 × China97−2]$_{F6-14}$ | 8.55$^{f}$ | 4.77$^{c}$ | 62.82$^{ef}$ | 16.75$^{i}$ | 1.88$^{c}$ | 1.03$^{f}$ | 2.77$^{def}$ | 1.05$^{e-h}$ | 43.78$^{f-i}$ | 3.83$^{ef}$ | 83.83$^{j}$ | 4.25$^{g}$ |
| [(NC17090 × B1)-25 × KK60−3]$_{F6-7-4}$ | 9.28$^{e}$ | 3.85$^{hi}$ | 62.18$^{f}$ | 18.78$^{h}$ | 1.57$^{fg}$ | 0.90$^{g}$ | 2.28$^{gh}$ | 0.77$^{k}$ | 44.17$^{f-i}$ | 3.38$^{fg}$ | 86.73$^{h}$ | 4.58$^{ef}$ |
| (Luhua11 × China 97−2)$_{F5-13}$ | 10.05$^{d}$ | 4.43$^{de}$ | 57.07$^{h}$ | 23.53$^{f}$ | 1.48$^{g}$ | 0.77$^{h}$ | 1.85$^{i}$ | 0.90$^{ij}$ | 44.37$^{e-i}$ | 2.52$^{g}$ | 90.43$^{f}$ | 4.33$^{g}$ |
| **Low-Oleic Acid Group** | | | | | | | | | | | | |
| Tainan 9 | 13.05$^{a}$ | 4.07$^{fgh}$ | 40.50$^{m}$ | 36.15$^{a}$ | 1.63$^{def}$ | 0.77$^{h}$ | 2.88$^{cde}$ | 0.92$^{i}$ | 43.57$^{ghi}$ | 1.12$^{h}$ | 98.02$^{a}$ | 3.43$^{ij}$ |
| KK 5 | 12.60$^{b}$ | 4.37$^{def}$ | 42.37$^{jk}$ | 35.78$^{ab}$ | 1.63$^{def}$ | 0.80$^{h}$ | 2.87$^{cde}$ | 0.78$^{k}$ | 43.28$^{hi}$ | 1.20$^{h}$ | 99.00$^{a}$ | 3.52$^{i}$ |
| KKU 1 | 11.32$^{c}$ | 5.87$^{a}$ | 41.32$^{lm}$ | 33.45$^{d}$ | 2.28$^{a}$ | 0.73$^{hi}$ | 3.25$^{a}$ | 1.00$^{f-i}$ | 47.18$^{ab}$ | 1.23$^{h}$ | 94.08$^{e}$ | 3.22$^{k}$ |
| KKU 40 | 12.30$^{b}$ | 4.03$^{ghi}$ | 42.75$^{j}$ | 34.20$^{c}$ | 1.70$^{d}$ | 0.90$^{g}$ | 3.25$^{a}$ | 1.02$^{e-i}$ | 44.70$^{d-h}$ | 1.23$^{h}$ | 96.67$^{b}$ | 3.48$^{ij}$ |
| KK 60−1 | 12.50$^{b}$ | 4.33$^{d-g}$ | 43.28$^{j}$ | 33.87$^{cd}$ | 1.68$^{de}$ | 0.75$^{hi}$ | 2.75$^{def}$ | 0.77$^{k}$ | 45.60$^{b-f}$ | 1.27$^{h}$ | 96.48$^{bc}$ | 3.52$^{i}$ |
| KK 60−2 | 12.67$^{ab}$ | 6.02$^{a}$ | 39.17$^{n}$ | 35.38$^{b}$ | 2.22$^{a}$ | 0.67$^{i}$ | 3.18$^{ab}$ | 0.95$^{ghi}$ | 42.65$^{i}$ | 1.10$^{h}$ | 95.45$^{cd}$ | 3.02$^{l}$ |
| KK 4 | 12.30$^{b}$ | 4.62$^{cd}$ | 41.78$^{kl}$ | 33.72$^{cd}$ | 1.88$^{c}$ | 0.80$^{h}$ | 3.23$^{a}$ | 1.05$^{d-h}$ | 46.33$^{bcd}$ | 1.23$^{h}$ | 94.97$^{de}$ | 3.32$^{jk}$ |
| Kalasin 2 | 13.05$^{a}$ | 2.37$^{l}$ | 47.22$^{i}$ | 31.28$^{e}$ | 1.15$^{i}$ | 1.25$^{e}$ | 2.80$^{def}$ | 1.40$^{a}$ | 40.52$^{j}$ | 1.53$^{h}$ | 95.75$^{bcd}$ | 3.87$^{h}$ |
| *F* test | **[a] | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** | ** |

[a] ** Significant at $p \leq 0.01$, means in the same column followed by the same letter (s) are not significantly different (at $p < 0.05$) by DMRT.

was the lowest in the rainy season of 2007 (**Table 4**). Dry season favors the production of linoleic acid than oleic acid. This could be due to lower temperature during pod filling phase in the dry season (data not shown) as low soil temperature increases the activity of enzyme Δ12 desaturase that is responsible for the production of linoleic acid (*15*, *17*, *18*). The seasonal differences for most characters were not unexpected because fatty acid compositions are affected by environmental factors. The variations in genotype, year, season, location, drought stress, and soil temperature could affect percent of fatty acid compositions (*15*−*18*). In this study, however, arachidic, behenic acids, % oil, and U/S ratio were not significantly affected by seasonal variation and showed to be more stable than the other characters.

Genotypic differences were further partitioned into three groups with different levels of oleic acid compositions. High variations in fatty acid compositions were found among three groups and within intermediate and low groups, whereas the high group had low variations for most characters except for linoleic, eicosenoic acids, O/L ratio, IV, and U/S ratio (**Tables 2** and **3**). Moreover, the variations among groups in oleic, linoleic acids, and O/L ratio

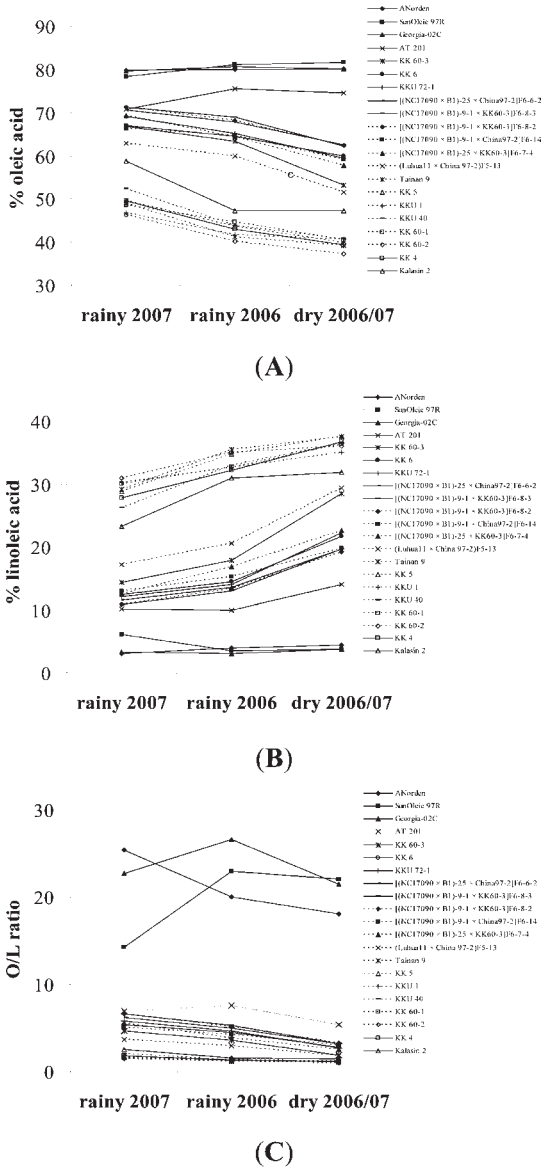


**Figure 1.** Percentage of oleic acid (**A**), linoleic acid (**B**), and O/L ratio (**C**) for the rainy seasons 2006 and 2007 and the dry season 2006/07 averaged over 21 peanut genotypes.

accounted for 87, 86, and 92% of total variation, respectively. The results indicated that selection among groups for these traits should be most effective. Percentages of oleic acid content for genotypes in high group were 80.02−81.32% on the average over three seasons, whereas wider ranges were found for intermediate and low groups, ranging from 57.07−75.20% and 39.17−48.22%, respectively (**Table 5**). The high variation for fatty acid compositions could be due to large differences in fatty acid compositions among groups. In contrast to the variation among groups, the variations in fatty acid compositions within groups were smaller largely due to the fact that peanut genotypes within groups clustered together. These behaviors observed in the range of peanut genotypes in this study are due to the genotypic differences for oleic acid in different groups, whereas the lines within the same groups had common genotype, for example, $ol_1ol_1ol_2ol_2$ for the high group, $ol_1ol_1Ol_2Ol_2$ or $Ol_1Ol_1ol_2ol_2$ for the intermediate group, and $Ol_1Ol_1Ol_2Ol_2$ for the low group (*9*, *10*).

Significant G × E interactions were found for all characters under study (**Tables 2** and **3**). The interactions were further partitioned into the interactions among groups and the interactions among genotypes within groups. The interaction among groups was the main source of G × E interactions for palmitic, oleic, linoleic, eicosenoic acids, O/L ratio, IV, and U/S ratio, accounting for more than half of total sum of squares. The high group was rather isolated from the rest and thus the interactions among groups occurred largely between intermediate and low groups for oleic, linoleic, and O/L ratio (**Figure 1**). As the high group was rather separated from the other groups and it had low G × E interaction, selection for high-oleic would be highly effective. Although the conclusion was limited to few genotypes, this information is very useful for breeding for high-oleics. However, the interactions among groups for % oil were not significant, indicating that the ranks of the groups did not change across seasons.

The interaction among peanut genotypes within high groups in general was less important except for linoleic, behenic, lignoceric acid, % oil, O/L ratio, IV, and U/S ratio that showed significant interactions (**Tables 2** and **3**). The interaction among genotypes within high group was not likely to be an important source of total interaction because the ranges of fatty acids of the high group were rather close compared to wider ranges for low and intermediate groups.

The interaction of peanut genotypes within the intermediate-oleic group was an important source of total interactions for all traits, except eicosenoic acid and O/L ratio, especially for % oil that accounted for more than half of total interaction sum of square. The interaction of peanut genotypes within low group was also important source of total interaction for all traits, except

**Table 6.** Biomass, Pod Yield, and Harvest Index (HI) for 21 Peanut Genotypes Averaged over Three Seasons

| peanut genotypes | (kg/ha) biomass | (kg/ha) pod yield | HI |
|---|---|---|---|
| **High-Oleic Acid Group** | | | |
| ANorden | $6267^{g-j}$ | $1133^{ij}$ | $0.17^{efg}$ |
| SunOleic 97R | $6450^{f-j}$ | $1345^{gh}$ | $0.21^{c-g}$ |
| Georgia-02C | $7116^{e-h}$ | $1675^{e}$ | $0.24^{b-f}$ |
| mean of group | 6611 | 1384 | 0.20 |
| **Intermediate-Oleic Acid Group** | | | |
| AT 201 | $5514^{ij}$ | $1212^{hij}$ | $0.20^{c-g}$ |
| KK 60−3 | $8625^{bc}$ | $2052^{bc}$ | $0.25^{bcd}$ |
| KK 6 | $8651^{bc}$ | $2226^{ab}$ | $0.26^{bcd}$ |
| KKU 72−1 | $8727^{bc}$ | $2183^{ab}$ | $0.26^{bc}$ |
| $[(NC17090 \times B1)\text{-}25 \times China97\text{-}2]_{F6-6-2}$ | $8530^{bc}$ | $1994^{bc}$ | $0.24^{b-e}$ |
| $[(NC17090 \times B1)\text{-}9\text{-}1 \times KK60\text{-}3]_{F6-8-3}$ | $8189^{b-e}$ | $1680^{e}$ | $0.21^{c-g}$ |
| $[(NC17090 \times B1)\text{-}9\text{-}1 \times KK60\text{-}3]_{F6-8-2}$ | $8241^{b-e}$ | $2364^{a}$ | $0.30^{b}$ |
| $[(NC17090 \times B1)\text{-}9\text{-}1 \times China97\text{-}2]_{F6-14}$ | $9836^{a}$ | $2181^{ab}$ | $0.22^{c-f}$ |
| $[(NC17090 \times B1)\text{-}25 \times KK60\text{-}3]_{F6-7-4}$ | $9139^{ab}$ | $1938^{c}$ | $0.22^{c-f}$ |
| $(Luhua11 \times China\ 97\text{-}2)_{F5-13}$ | $5976^{hij}$ | $2222^{ab}$ | $0.37^{a}$ |
| mean of group | 8143 | 2005 | 0.25 |
| **Low-Oleic Acid Group** | | | |
| Tainan 9 | $6454^{f-j}$ | $1047^{j}$ | $0.16^{fg}$ |
| KK 5 | $8406^{bcd}$ | $1711^{de}$ | $0.20^{c-g}$ |
| KKU 1 | $6639^{f-i}$ | $1491^{efg}$ | $0.21^{c-g}$ |
| KKU 40 | $7533^{c-f}$ | $1920^{cd}$ | $0.25^{bcd}$ |
| KK 60−1 | $7258^{d-g}$ | $1599^{ef}$ | $0.22^{c-g}$ |
| KK 60−2 | $5367^{j}$ | $985^{j}$ | $0.18^{d-g}$ |
| KK 4 | $8295^{b-e}$ | $1416^{fgh}$ | $0.17^{efg}$ |
| Kalasin 2 | $6785^{fgh}$ | $1039^{j}$ | $0.14^{g}$ |
| mean of group | 7092 | 1401 | 0.19 |
| *F* test | **[a] | ** | ** |

[a] ** Significant at $p \leq 0.01$, means in the same column followed by the same letter (s) are not significantly different (at $p < 0.05$) by DMRT.

**Table 7.** Correlation Coefficient between Fatty Acid Compositions, % Oil, The Ratio of Oleic to Linoleic Acid (O/L Ratio), Iodine Value (IV), the Ratio of Unsaturated to Saturated Fatty Acid (U/S Ratio), Biomass, Pod Yield, And Harvest Index (HI) for Three Seasons of 21 Peanut Genotypes[a]

| | palmitic acid | stearic acid | oleic acid | linoleic acid | arachidic acid | eicosenoic acid | behenic acid | lignoceric acid | % oil | O/L ratio | IV | U/S ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pod yield | −0.23** | 0.05 | 0.08 | −0.07 | 0.05 | −0.04 | 0.01 | −0.03 | 0.35** | −0.15 | −0.06 | 0.04 |
| biomass | −0.01 | −0.05 | −0.05 | 0.05 | −0.01 | −0.1 | 0.03 | −0.36** | 0.08 | −0.21* | 0.07 | −0.04 |
| HI | −0.28** | 0.11 | 0.14 | −0.13 | 0.07 | −0.03 | −0.05 | 0.17 | 0.33** | −0.06 | −0.13 | 0.07 |

[a] *,** Significant at $p \leq 0.05$ and 0.01 probability levels, respectively.

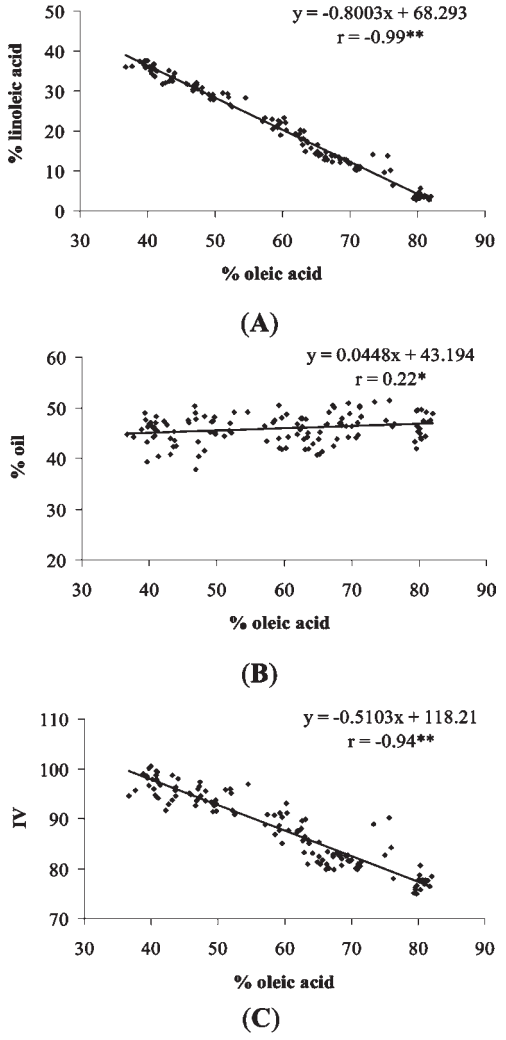


**Figure 2.** Relationships between oleic acid and linoleic acid (**A**), % oil (**B**), and iodine value (IV) (**C**) in peanut genotypes.

eicosenoic acid, O/L ratio, and U/S ratio. The G × E interactions for oleic acid among peanut groups were observed between intermediate- and low-oleic acid groups only. This could be due to the high influence of modifier genes on oleic acid in low and intermediate groups. In the high group, the expression of the double recessive genes ($ol_1$ and $ol_2$) could mask the expression of modifier genes (*10*).

As can be seen in **Figure 1A** for oleic acid, the peanut genotypes in the high group performed similarly and the genotypes in the low group followed similar pattern of performance in which oleic acid increased in all genotypes in the rainy season 2007. The high interaction occurred in the intermediate group when most genotypes increased oleic acid, but the genotypes AT 201 decreased oleic acid in the rainy season 2007. The interactions for linoleic acid were in a reverse pattern of those for oleic acid (**Figure 1A**,**B**). This could be due to negative relationship of the two types of fatty acids. Again, the high interaction was still in the intermediate group. The significant interaction for O/L ratio was observed in the high group. The significant interaction was caused by high O/L ratio of the line ANorden in the rainy season 2007, but in other seasons, it had lower O/L ratio than did SunOleic 97R and Georgia-02C (**Figure 1C**). Another possible explanation for the significant interaction for O/L ratio is that this character is more sensitive than oleic and linoleic acids.

Considerable variations due to G × E interactions were observed for biomass, pod yield, and harvest index (HI), accounting for 30, 18, and 15% of total variation, respectively (**Table 3**). The results were in agreement with those reported by Phakamas (*22*). The lower G × E interactions for oleic acid is possibly due to the more simple genetic control of the traits compared to more complex inheritance for biomass, pod yield, and HI.

High yield has always been an important consideration for any breeding program. The peanut genotypes with high-oleic acid should also possess good agronomic traits contributing to high pod yield. The genotypes with top yield and biomass production were mostly in the intermediate-oleic group (**Table 6**). For the high-oleic group, yield of Georgia-02C is slightly higher than other lines in the group although it was not as high as the top yielding lines in intermediate group. The relationships between fatty acid compositions and agronomic characters were presented in **Table 7**. Correlations between oleic acid and pod yield ($r$ = 0.08), between oleic acid and biomass ($r = -0.05$), and between oleic acid and HI ($r$ = 0.14) were not significant. The correlation between oleic acid and pod yield was not significant, indicating independent segregation of these traits. The lack of associations between oleic acid and pod yield suggested that improvement of individual traits is possible.

Oleic acid was inversely correlated with linoleic acid ($r = -0.99$, $p \leq 0.01$) and IV ($r = -0.94$, $p \leq 0.01$) and positively correlated with % oil ($r$ = 0.22, $p \leq 0.05$) (**Figure 2**). The results were in agreement with previous reports (*2*, *15*, *16*), who found negative relationship ($r = -0.99$, $p \leq 0.01$) between oleic and linoleic acids. The relationships of fatty acid compositions are regulated by genes encoding for enzymes involved in fatty acid biosynthesis, and up or down regulations of these enzymes are influenced by environment conditions (*15*, *18*, *23*, *24*).

In conclusion, genotypic variation was the main source of variation for fatty acid composition and significant genotype × environment (G × E) interactions for oleic acid were found mostly among peanut genotypes in low and intermediate groups. However, nonsignificant G × E interactions were found in the high group, indicating that the high group is less affected by environmental changes and, therefore, selection for high-oleic acid will be effective.

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