M.G. Stephenson. 1993. 1992 Field crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, and summer annual forages. Res. Rept. 618, University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, R.B. Bennet, R.D. Gipson, S.H. Baker, W.D. Branch, and M.G. Stephenson. 1992. 1991 Field crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, and summer annual forages. Res. Rept. 609, University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, A.E. Coy, S.H. Baker, W.D. Branch, and S.H. LaHue. 1997. 1996 Field crops performance tests: Soybean, peanut, cotton, tobacco, sorghum, grain millet and summer annual forages. Res. Rept. 644. University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, A.E. Coy, S.H. Baker, W.D. Branch, and M.G. Stephenson. 1996. 1995 Field crops performance tests: Soybean, peanut, cotton, tobacco, sorghum, grain millet, and summer annual forages. Res. Rept. 639. University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, A.E. Coy, S.H. Baker, W.D. Branch, and M.G. Stephenson. 1995. 1994 Field crops performance tests: Soybean, peanut, cotton, tobacco, sorghum, grain millet, and summer annual forages. Res. Rept. 633. University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, C.D. Fisher, and R.H. Heyerdahl. 1989. 1988 Field crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, summer annual forages, and sunflowers. Res. Rept. 568, University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, C.D. Fisher, and R.H. Heyerdahl. 1988. 1987 Field Crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, summer annual forages, and sunflowers. Res. Rept. 556, University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, R.D. Gipson, S.H. Baker, W.D. Branch, and M.G. Stephenson. 1991. 1990 Field crops performance tests: Soybeans, peanuts, cotton, tobacco, sorghum, and summer annual forages. Res. Rept. 599, University of Georgia, Athens, GA.
Raymer, P.L., J.L. Day, and R.D. Gipson. 1990. 1989 Field crops performance tests. Res. Rept. 589, University of Georgia, Athens, GA.
Ritchie, J.T., D.C. Godwin, and U. Singh. 1989. Soil and water inputs for the IBSNAT models. p. 31–45. *In* Proceedings of IBSNAT Symposium: Decision Support System for Agrotechnology Transfer. University of Hawaii, Honolulu, HI.
Specht, J.E., J.H. Williams, and C.J. Weidenbenner. 1986. Differential responses of soybean genotypes subjected to a seasonal soil water gradient. Crop Sci. 26:922–934.
Tsuji, G.Y., G. Uehara, and S. Balas (ed). 1994. DSSAT version 3. University of Hawaii, Honolulu, HI.
Willmott, C.J. 1982. Some comments on the valuation of model performance. Bull. Am. Meteorological Soc. 63:1309–1313.

Genetic Factors Influencing High Oleic Acid Content in Spanish Market-Type Peanut Cultivars

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ABSTRACT

Increasing the ratio of oleic to linoleic acid (O/L) in peanut (*Arachis hypogaea* L.) significantly improves the nutritional and quality attributes of the crop. In currently grown cultivars, the O/L ratio ranges from 0.8 to 2.5. Variation in peanut for O/L ratio has been characterized, and the O/L ratio is digenically inherited at two loci designated as Ol_1 and Ol_2. Previous research has been conducted with Virginia- and runner-type peanut; however, there have been no reports regarding the inheritance and allele frequency at these loci in Spanish-type peanut. The objectives of this study were to determine if the inheritance of the high oleate trait in Spanish-type peanut is similar to that previously reported and to determine the allelic composition of Spanish-type peanut at Ol_1 and Ol_2. Six different Spanish-type peanut cultivars (low oleate) were hybridized with F435-2—2 (high oleate). F_2 and BC_1F_1 progenies were evaluated for the O/L ratio. Segregation patterns indicated that high oleic acid content is digenically inherited in Spanish-type peanut, but there seems to be more allelic variation both within and among these cultivars. In addition, variation within the high and low oleate ratio classes indicated that other factors may be involved in determining the precise O/L ratio.

Peanut is a globally important protein and oilseed crop. In the USA, peanut is used primarily for food, but throughout the rest of the world, it is utilized as an oilseed crop (McWatters and Cherry, 1982). Like most edible oils, peanut oil is subject to oxidation which results in rancidity. Consequently, the shelf-life of products which contain peanut and peanut oil is limited. Improvements in quality and stability of peanut oil may improve the market value (Knauft and Ozias-Akins, 1995).

The oxidative stability and shelf-life of oil is influenced by the concentrations of specific fatty acids (Fore et al., 1953; Sanders, 1980a,b). In general, saturated fatty acids are less susceptible to oxidation than less saturated fatty acids. Two fatty acids, oleic and linoleic, comprise over 80% of the oil content of peanut. Of these, linoleic acid is less saturated and less stable than oleic acid. Holley and Hammons (1968) reported a strong negative correlation between linoleic acid content and oil stability in peanut. Robertson and Thomas (1976) reported that oil with higher ratios of oleic to linoleic acid retains its quality longer in the seed or as oil. Gorbet and Knauft (1997) found that 'SunOleic 95R', a high oleic runner cultivar, had much longer shelf-life than the traditional runner-type peanut cultivars.

In addition to increasing the stability of peanut oil, increasing the O/L ratio in peanut appears to have health benefits as well. Research has associated high oleic acid with lowered blood serum cholesterol, especially low-density lipoproteins (LDL) in humans (O'Bryne et al., 1997). Renaud et al. (1995) reported a 70% decrease in recurrent myocardial effects when oleic acid levels are increased in plasma fatty acids.

Increasing the O/L ratio in peanut seems to have positive effects on peanut quality and nutritional value. The majority of peanut cultivars average 55% oleic acid and 25% linoleic acid (Knauft et al., 1993). Norden et al.

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Abbreviations: BHT, butylated hydroxytoluene; GC, gas chromatography; IDBLs, independent derived backcross lines; LDL, low-density lipoproteins; O/L, oleic to linoleic acid ratio; TAES, Texas Agricultural Experiment Station.

(1987) evaluated over 500 genotypes to determine the range in oleic and linoleic acid in peanut germplasm. They identified a breeding line with 80% oleic acid and 2% linoleic acid. The relationship between the two fatty acids is directly related so that expressing the O/L ratio accurately reflects the relative contents of these two fatty acids in peanut (Knauft et al., 1993).

Early investigations indicated that the fatty acid composition of peanut is quantitatively inherited (Khan et al., 1974; Mercer et al., 1990; Mason and Matlock, 1967; Tai, 1972; Tai and Young, 1975). More recently, Moore and Knauft (1989) found that two loci, designated *Ol*$_1$ and *Ol*$_2$, controlled the high O/L ratio in runner and Virginia-type peanut cultivars. Isleib et al. (1996) surveyed five different cultivars of Virginia-type peanut for their allelic composition at *Ol*$_1$ and *Ol*$_2$ and found that four of the Virginia-type peanut cultivars were either *Ol*$_1$*Ol*$_1$*ol*$_2$*ol*$_2$ or *ol*$_1$*ol*$_1$*Ol*$_2$*Ol*$_2$ and one was *Ol*$_1$*Ol*$_1$*Ol*$_2$*Ol*$_2$. Inheritance of the high oleate trait or the allele frequencies of Spanish-type peanut cultivars at the *Ol*$_1$ and *Ol*$_2$ loci have not been reported.

Spanish-type peanut is still grown in Texas because it is earlier maturing and more drought tolerant than other market types. In addition, the candy industry prefers Spanish-type peanut because of its smaller size and flavor characteristics. Unfortunately, because Spanish-type cultivars have lower O/L ratios, the oil is less stable than oil from either runner or Virginia-type peanut cultivars (Picket and Holley, 1951; Jamieson et al., 1921).

The peanut breeding program at Texas A&M University has been working to develop Spanish-type peanut cultivars with high oleic acid content. Early in the breeding process, significant variation and variable segregation patterns were observed in the crosses of low oleate Spanish type with F435-2—2, the high oleate line (Norden et al., 1987). The objectives of this study were (i) to determine if the inheritance of the high oleic acid trait in Spanish-type peanut is similar to that reported in runner and Virginia-type peanut and (ii) determine the allelic composition of Spanish-type peanut at the loci controlling the inheritance of this trait.

MATERIALS AND METHODS

Germplasm Development

Six Spanish-type peanut cultivars with low O/L ratios were hybridized as females to F435-2—2, the high O/L line, to create segregating populations for genetic analysis. The six low O/L ratio Spanish-type cultivars represent an array of breeding types from different locations (Table 1). F435-2—2 is a strain from the F435 population that was identified at the University of Florida as high O/L by Norden et al. (1987) and is classified as a Spanish-type peanut. Two reciprocal F_1 crosses with F435-2—2 as a female and 'Tamspan 90' (Smith et al., 1991) and 'Starr' (Simpson, 1972) as males were included to check for maternal effects.

Table 1. Identification, type, origin, and oleic to linoleic acid ratio (O/L) of the six low O/L peanut cultivars and the high O/L ratio peanut breeding line included in the inheritance study.

Name	Type	Origin	Average O/L ratio
Tamspan 90	Cultivar	USA	1.3
Starr	Cultivar	USA	1.1
Spanco	Cultivar	USA	1.1
TS 32-1	Cultivar	Africa	1.0
55-437	Cultivar	Africa	1.0
Fleur 11	Cultivar	China	1.1
F435-2—2	Breeding Line	USA	34.0

Peanut plants were grown in both the greenhouse and field under standard procedures. During the spring of 1996 and 1997, crosses were made in the greenhouse at College Station, TX, by the standard artificial hybridization procedure for peanut (Knauft et al., 1987). F_1 seeds were planted in the field in June of the respective years and F_2 seeds were separated by individual plants. The number of F_2 seed from some individual F_1 plants was too small to be analyzed independently, so data from several plants were pooled. When enough F_2 seeds from individual F_1 plants were available, they were analyzed independently. Data were pooled when a test of homogeneity indicated no differences among $F_{1:2}$ progenies (Strickberger, 1976). Because recent studies have shown little genotype × environment action effect on the *Ol*$_1$ and *Ol*$_2$ loci (A.M. Schubert and O.D. Smith, 1994, personal communication), data from crosses in a population were pooled across environments if heterogeneity among families was not detected. For four of the six crosses [Tamspan 90, Starr, 'Spanco' (Kirby et al., 1989), and 'TS 32-1' (Bockelée-Morvan, 1983b)], a backcross to the high O/L parent was made to create a segregating BC_1F_1 population. Plants were harvested at maturity on the basis of the hull-scrape method (Williams and Drexler, 1981). Oil was extracted from segments of seed from the parents, F_1, F_2, and BC_1F_1 generations. These samples were analyzed for oleic and linoleic acid content by gas chromatography (GC) (see oil analysis). After classifying progenies as having high O/L or low O/L ratios, segregation patterns were examined for genetic interpretation. Chi-square analysis was used to test conformity to the expected segregation patterns.

For each population, oil samples from the respective parents were measured in the GC autosampler after every 20 F_2 oil samples to obtain a range of values for the parents compared with the values of individual F_2 progeny. For each of the original single-cross segregating populations, a minimum of 145 F_2 seeds from at least two plants in each population were analyzed to determine segregation ratios. In addition, a minimum of 40 F_2 seeds were tested for the two reciprocal crosses. For the BC_1F_1 populations, at least 20 seeds were analyzed. Any seeds that were obviously small or immature were not included in the analysis.

To evaluate further low-intermediate O/L individuals, a set of independently derived backcross lines (IDBLs) were developed. The IDBLs were derived from the BC_1 generation of the cross Tamspan 90 × (Tamspan 90 × F435-2—2). Plant-row populations from this BC_1 were planted at College Station, TX. Ten seed samples from each plot were analyzed for O/L ratio. Individual plants from plant rows with values slightly higher than those of the low parent (2.0 to 4.5, designated "low intermediate"), and values in the lower range of high O/L parent (9.0 to 15), were selected for low and high O/L ratio, selfed, and advanced to the F_9 generation. Ten to 20 seeds of each of the 10 IDBLs were analyzed for O/L.

Oil Analysis

For each sample, a piece of the distal end of one cotyledon from the nonembryo end of the seed was detached, the testa removed, and stored in a 0.5-mL microcentrifuge tube at −20°C. The rest of the seed was saved for planting. Samples were extracted by adding 2 mL hexane with 0.01% (v/v) butylated hydroxytoluene (BHT) and vortexed. A boiling chip was

added, along with 2 mL H_2SO_4:methanol (1:99) and vortexed. Samples were placed in a heat block at 90°C until 0.5 mL of solution was left in the tube. The samples were allowed to cool to room temperature. Two milliters hexane with 0.01% BHT were added. The samples were vortexed and held at room temperature for 30 min. The organic phase was transferred to a preweighed, capped vial. The solvent was evaporated under a fume hood with a stream of nitrogen gas. The tubes with the extracted oil were weighed and the exact weight of the oil sample was calculated. The sample was dissolved in ethyl acetate to a concentration of approximately 1 μg/μL. The sample was contained in a 2 mL borosilicate glass vial.

Two microliters were injected into a GC for each analysis. Injector and detector temperatures were set at 250°C. The oven was programmed for an initial temperature setting of 95°C for 2 min, then increased at a rate of 1.8°C per min until reaching a temperature of 130°C and held for 3 min. The temperature was increased at a rate of 10°C per min to a maximum of 150°C. The column was an Rtx-2330 (30 m, 0.53 mm, and 0.2-μm film thickness, Restek Corporation, Bellefonte, PA). A flame ionization detector was used. Standard methyl ester fatty acid mixtures (AOCS-2, Sigma, St. Louis, MO) were used to identify the fatty acids by comparison of their retention times. The fatty acids are reported as the proportion of oleic to linoleic acid.

RESULTS AND DISCUSSION

All six Spanish-type peanut cultivars designated as low O/L ratio had O/L ratios ranging from 0.8 to 2.1 with an average O/L ratio of 1.2, while F435-2—2 had an average O/L ratio of 34.0 with a range of 14.0 to 45.0 (Table 2). The O/L ratio of F_1 hybrids ranged from 1.0 to 3.6 (Table 2) indicating that low O/L ratios were dominant to high O/L ratios. Segregation was observed in all six F_2 populations with O/L ratios ranging from 0.8 to 48.8. The majority of the F_2 progeny had O/L ratios that were less than 5.0 (Fig. 1). In all six F_2 populations, including the two reciprocals, there were values for O/L ratios that were slightly higher than those of the low parent (e.g., 1.8–4.5), but these ratios were much lower than those of the high parent. Because these low-intermediate types were much closer in O/L ratio to the low parent, they were classified as low O/L individuals for the purpose of determining segregation patterns. This classification is justified on the basis of the absence of individuals with O/L ratios between 6.0 to 9.0. Any individual with a O/L ratio greater than 10.0 was classified as high O/L.

On the basis of previous reports, segregation ratios of either 3:1 or 15:1 (low O/L:high O/L) were expected in the F_2 progeny which are indicative of monogenic and digenic inheritance, respectively (Moore and Knauft, 1989). In the first backcross to the high oleate parent, segregation ratios of either 1:1 or 3:1 were expected, depending on the genetics of the low oleate parent (Moore and Knauft, 1989; Knauft et al., 1993).

Three of the six segregating populations produced data very consistent with a 15:1 segregation ratio. The F_2 populations from the crosses of Tamspan 90, '55-437' (Bockeleé-Morvan, 1983a), and 'Fleur 11' (Mortreuil, 1993) by F435-2—2 all fit the expectations of digenic inheritance (Table 3). A BC_1F_1 population of Tamspan 90 also fit the expected segregation ratios of digenic inheritance and did not fit the expected ratios for monogenic inheritance (Table 4).

In the cross of Starr × F435-2—2, F_2 progeny from five F_1 plants were evaluated. In four of the five plants, segregation patterns were consistent, and bulked data fit expectations of digenic inheritance, but not for monogenic inheritance (Table 5). One F_1 plant (No. 442) produced an F_2 population that did not fit either model. The exact cause of this variant segregation is not known, but it may be due to sampling, contamination, or the presence of genetic modifiers influencing the trait. If the latter is true, this indicates that the cultivar Starr is variable for factors influencing O/L ratio. The majority of the data in this cross support the expected ratios for digenic inheritance.

No differences in segregation pattern were observed for the two reciprocal F_2 populations, with F435-2—2 as a female and Tamspan 90 and Starr as males (Tables 3 and 5). This suggests that no interaction occurs between nuclear and extranuclear factors for the high oleate trait

Table 2. Spanish-type peanut cultivars, F435-2—2, their crosses, and the respective oleic to linoleic acid ratio (O/L) ranges.

Cross	Female parent	F_1	F_2	BC_1F_1
Tamspan 90 × F435-2—2	0.9–2.1†	1.4–3.0	0.8–39.4	1.7–42.4
Starr × F435-2—2	1.0–1.3	1.1–1.9	0.9–44.4	1.7–35.2
55-437 × F435-2—2	1.0–1.3	1.2–2.3	0.8–26.3	–
Fleur 11 × F435-2—2	1.0–1.3	1.2–2.3	0.9–27.8	–
TS 32-1 × F435-2—2	0.9–1.8	1.6–3.6	0.9–42.6	1.2–48.1
Spanco × F435-2—2	0.8–1.8	1.0–2.2	0.8–48.8	1.4–41.5
F435-2—2	14.0–45.0			

† The data presented are the range in oleic relative to a linoleic acid value of 1.0.

Table 3. Segregation for oleic to linoleic acid ratio (O/L) of F_2 peanut populations and χ^2 values for the crosses of Tamspan 90, 55-437, and Fleur 11 with F435-2—2.

Cross	No. of seed		Two-gene χ^2 (15:1)	One-gene χ^2 (3:1)
	Low O/L	High O/L		
Tamspan 90 × F435-2—2	395	25	0.12†	81.77**
F435-2—2 × Tamspan 90	74	2	2.29	20.89**
55-437 × F435-2—2	150	9	0.21	32.24**
Fleur 11 × F435-2—2	134	11	0.27	23.92**

** Denote significance at the 0.01 probability level.
† All the χ^2 values were compared for 1 df and computed with Yates correction.

Table 4. Segregation for oleic to linoleic acid ratio (O/L) of BC_1F_1 peanut populations and χ^2 values for the crosses of Tamspan 90, Starr, Spanco, and TS 32-1 with F453-2—2.

Cross	No. of seed		Two-gene χ^2 (3:1)	One-gene χ^2 (1:1)
	Low O/L	High O/L		
F435-2—2 × (Tamspan 90 × F435-2—2)	48	26	3.8†	6.0*
F435-2—2 × (Starr × F435-2—2)	16	4	0.07	7.2**
F435-2—2 × (Spanco × F4352—2)	15	5	0.06	5.0*
F435-2—2 × (TS 32-1 × F435-2—2)	16	4	0.07	7.2**

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.
† All the χ^2 values were compared for 1 df and computed with Yates correction.

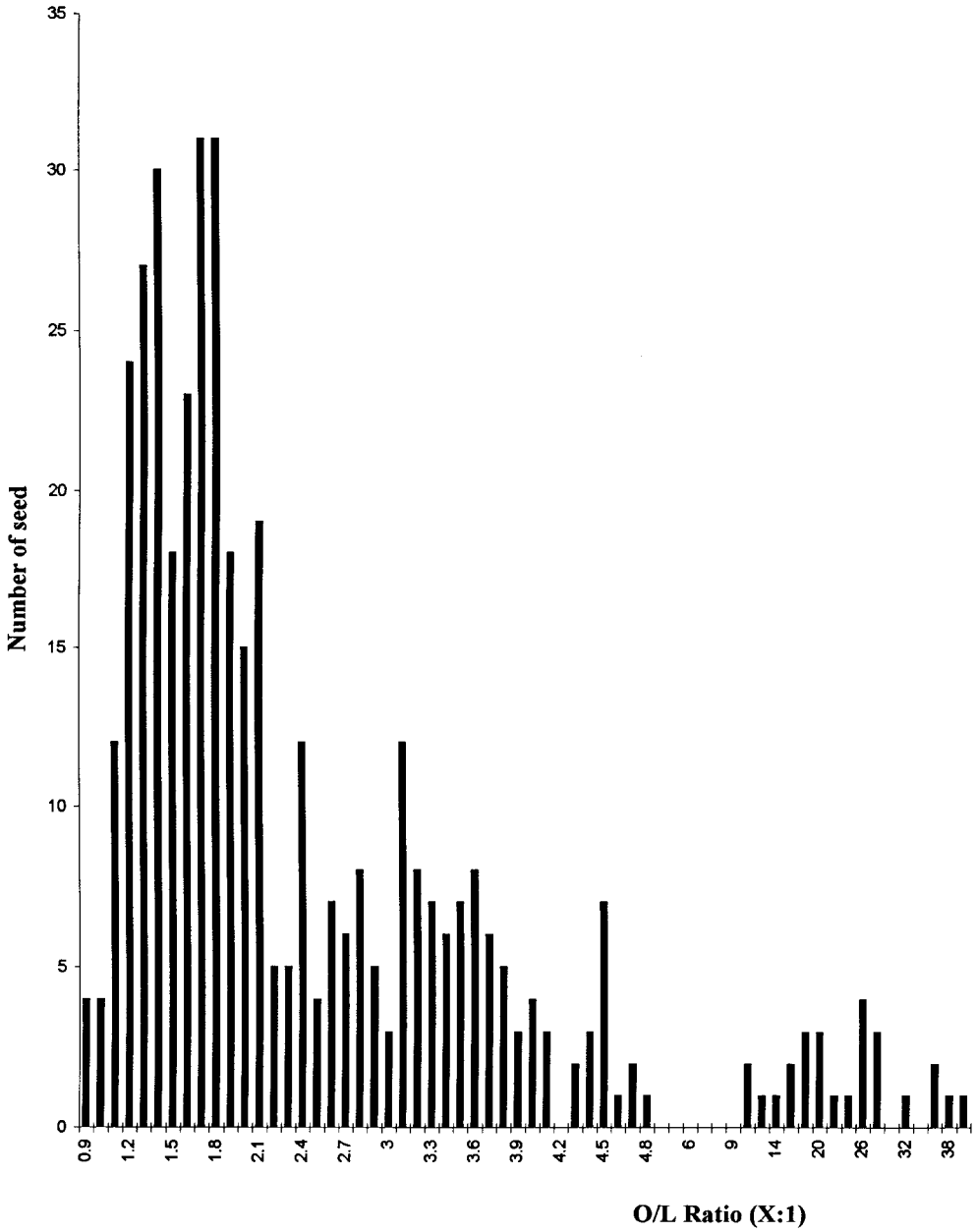

Fig. 1. Frequency distribution of oleic to linoleic acid ratio (O/L) in F_2 seed of Tamspan 90 × F435-2—2 (N = 420). The distribution was similar for most of the other F_2 populations. For presentation purposes, there is a change in the scale at O/L ratio of 5.0.

in these two Spanish-type cultivars. In addition, the consistency of data among families in a cross indicates that genotype × environment had little effect on the expression of *Ol*$_1$ and *Ol*$_2$ loci.

The results observed in the crosses Spanco and TS 32-1 by F435-2—2 indicate that Spanco and TS 32-1 are variable at the loci controlling O/L ratio. In the cross of Spanco × F435-2—2, a total of seven F_2 families were evaluated, and five of these families fit the expected ratios for digenic inheritance. BC_1F_1 populations were created using four of these families and the BC_1F_1 progeny segregation fit the expected ratios for digenic inheritance (Table 4). The remaining two F_2 families segregated in a manner consistent with monogenic inheritance (Table 5). In the cross of TS 32-1 × F435-2—2, a total of five F_2 families were evaluated and four of these families fit the expected ratios for digenic inheritance (Table 5). BC_1F_1 populations were created by means of these four families and segregation in the BC_1F_1 progeny fit the expected ratios for digenic inheritance (Table 4). The last F_2 family segregated in a manner consistent with monogenic inheritance (Table 5).

The data indicate that both Spanco and TS 32-1 fit the expected ratios for digenic inheritance for O/L ratio, but they are variable for the alleles present at the two loci involved in controlling the O/L ratio. On the basis of our observations of high and low O/L lines in the TAES breeding nurseries, these loci have no effect on the plant phenotype. Consequently, it is feasible that allelic variants could have been present at these loci

Table 5. Segregation for oleic to linoleic acid ratio (O/L) of F_2 peanut populations and χ^2 values for the crosses of Starr, Spanco, and TS 32-1 with F453-2—2.

Cross	Plant No.	No. of seed		Two-gene χ^2 (15:1)	One-gene χ^2 (3:1)
		Low O/L	High O/L		
Starr × F435-2—2	4 plants (pooled)	75	4	0.42†	17.29**
	442	138	25	18.60**	8.38**
F435-2—2 × Starr	455	36	4	0.51	5.23*
Spanco × F435-2—2	4 plants (pooled)	57	3	0.42	13.35**
	612	134	15	3.16	18.13**
	458	56	10	7.66**	3.69
	465	31	9	15.71**	0.23
TS 32-1	4 plants (pooled)	69	3	0.90	17.24**
	437	140	43	84.43**	0.31

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.
† All the χ^2 values were compared for 1 df and computed with Yates correction.

Table 6. Oleic to linoleic acid ratio (O/L) of individual peanut seed for the progeny of intermediate O/L plants that were allowed to self.

IDBL†	Parental O/L values	Progeny O/L values								
		0.8–3	3.1–6	6.1–9	9.1–12	12.1–15	15.1–18	18.1–21	21.1–24	24.1–27
1-16-1-4	9.7	0	0	2	6	1	1	0	0	0
1-16-2-2	7.4	0	0	3	3	2	2	0	0	0
1-16-2-4	8.0	0	0	2	2	5	0	0	0	0
1-16-2-5	7.2	0	1	6	7	2	3	1	0	0
1-16-8-4	10.3	0	0	0	6	3	1	0	0	0
3-35-9-5	4.5	6	4	0	0	0	0	0	0	0
3-35-9-6	4.0	2	5	0	0	0	0	2	1	0
3-35-11-5	4.6	0	0	1	1	5	1	0	0	2
3-35-13-3	6.5	1	8	0	0	0	1	0	0	0
3-35-13-6	4.3	3	5	0	0	0	1	0	0	1
Tamspan 90	1.3‡	30	0	0	0	0	0	0	0	0
F435-2—2§	34.0§	0	0	0	0	0	0	0	6	24

† IDBLs = independently derived backcross lines.
‡ Tamspan 90 had O/L values with a range from 0.9 to 2.1.
§ F435-2—2 had O/L values with a range from 20.4 to 38.6.

when the final selections were made prior to release. TS 32-1 is an African cultivar, which might indicate that some other Spanish-type cultivars from outside the USA also have one of the genes responsible for the high oleate trait in peanut.

The data presented in this study indicate that the O/L ratio in Spanish-type peanut is controlled by two genetic loci, but two observations indicate that modifiers or additional epistatic interactions may be occurring. First, in the cross of Starr × F435-2—2, one F_2 family segregated in a manner that did not fit any of the expected ratios (Table 5). Additional testing will be required to determine the cause of this different segregation ratio. Second, a significant number of F_2 progeny had O/L ratios that were slightly higher than their respective low O/L parent, but they were much closer to their low O/L parent than to the high O/L, F435-2—2 (Fig. 1). These low-intermediate O/L genotypes could have resulted from homozygous recessive genotypes at one locus and a dominant allele at the other locus ($ol_1ol_1Ol_2Ol_2$ or $Ol_1Ol_1ol_2ol_2$).

If these low intermediate values are considered a third category, then a 9 (low O/L) to 6 (intermediate O/L) to 1 (high O/L) segregation ratio would be expected. This ratio is indicative of duplicate interaction. When the data is partitioned in this manner, most of the F_2 populations that segregated for two genes showed good fit for the 9:6:1 ratio. On the basis of this logic, the plants that segregated at only one locus in Spanco and TS 32-1 should not produce any low F_2 progeny, but low O/L values were observed in these populations as well. In addition, since variation existed within the cultivars Spanco and TS 32-1, one would expect that intermediate values should be observed in individuals from these two cultivars. To verify this fact, approximately 75 seeds from both Spanco and TS 32-1 were assayed for O/L ratio and all of the individuals were low (0.9–1.8). Because of these inconsistencies, more research is necessary to determine the exact cause of these low- intermediate O/L ratios.

Progeny of self-low-intermediate lines was analyzed for O/L ratios. This information was used to determine the stabilizing of the intermediate O/L genotypes. Progeny from six of these IDBLs were very similar to their respective progenitor plants for O/L ratio (Table 6). For example, plant 1-16-1-4 had an original O/L value of 9.7. The 10 seeds analyzed among its progeny had O/L values ranging between 8.6 to 18.6, with 6 of the 10 plants classified in the range of 9.1 to 12.0. No low or extremely high O/L values were observed. The remaining four IDBLs showed significant variation in the O/L ratios of their progeny (Table 6). For example, plant 3-35-9-6, with an O/L ratio of 4.0, produced progeny with O/L values ranging from 2.2 to 25.4. These results suggest that some lines were "fixed" for those factors while others were not, probably indicating that modifiers are influencing the O/L ratio in these lines. Isleib et al. (1998) found that in addition to Ol_1 and Ol_2 other genetic factors influence O/L ratios. The data presented in our study support these findings, but addi-

tional research will be needed to determine the exact cause and mechanisms of control. Understanding the factors that cause intermediate O/L ratios may be relevant if there is a need to fix specific desired intermediate O/L ratios (e.g., 15:1).

The data presented in this study indicate that both the Ol_1 and Ol_2 loci control the high oleate trait in Spanish-type peanut; however, there is significant variability in the allelic composition at either or both loci within cultivars and this results in variable segregation patterns. In addition, the presence of low-intermediate O/L ratio genotypes indicates that other genetic modifiers may be involved in the expression of the O/L ratio in these genotypes.

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REFERENCES

Bockelée-Morvan, A. 1983a. The different varieties of groundnut. Geographical and climatic distribution, availability. Technical sheet for groundnut variety 55-437. Oléagineux 38:80.

Bockelée-Morvan, A. 1983b. The different varieties of groundnut. Geographical and climatic distribution, availability. Technical sheet for groundnut variety TS 32-1. Oléagineux 38:88.

Fore, S.P., N.J. Morris, C.H. Mack, A.F. Freeman, and W.G. Bickford. 1953. Factors affecting the stability of crude oils of 16 varieties of peanut. J. Am. Oil Chem. Soc. 30:298–301.

Gorbet, D.W., and D.A. Knauft. 1997. Registration of 'SunOleic 95R' Peanut. Crop Sci. 37:1392.

Holley, K.T., and R.O. Hammons. 1968. Strain and seasonal effects on peanut characteristics. Univ. Ga., Athens. Coll. Agric. Exp. Stn. Res. Bull. 32.

Isleib, T.G., C.T. Young, and D.A. Knauft. 1996. Fatty acid genotypes of five Virginia-type cultivars. Crop Sci. 36:556–558.

Isleib, T.G., R.F. Wilson, and W.P. Novitsky. 1998. Partial dominance, pleitropism, and epistasis in the inheritance of the high-oleate trait. p. 55. *In* J.R. Sholar and I. Nickles (ed.) Proc. Am. Peanut Res. and Educ. Soc., Inc., Norfolk, VA. 7–10 July 1998. American Peanut Research and Education Society, Oklahoma State University, Stillwater, OK.

Jamieson, G.S., W.F. Baughman, and D.H. Brauns. 1921. The chemical composition of peanut oil. J. Am. Chem. Soc. 43:1372.

Khan, A.R., D.A. Emery, and J.A. Singleton. 1974. Refractive index as basis for assessing fatty acid composition in segregating populations derived from intraspecific crosses of cultivated peanut. Crop Sci. 14:464–468.

Kirby, J.S., D.J. Banks, and J.R. Sholar. 1989. Registration of 'Spanco' peanut. Crop Sci. 29:1573–1574.

Knauft, D.A., K.M. Moore, and D.W. Gorbet. 1993. Further studies on the inheritance of fatty acid composition in peanut. Peanut Sci. 20:74–76.

Knauft, D.A., A.J. Norden, and D.W. Gorbet. 1987. Peanut breeding. p. 364–384. *In* W.R. Fehr (ed.) Principles of cultivar development. Vol 2. Macmillan Pub. Co., New York.

Knauft, D., and P. Ozias-Akins. 1995. Recent methodologies for germplasm enhancement and breeding. p. 54–94. *In* H.E. Pattee and H.T. Stalker (ed.) Advances in peanut science. Am. Peanut Res. and Educ. Soc., Inc. Stillwater, OK.

Mason, M.E., and R.S. Matlock. 1967. Progress report VII. Agronomic, organoleptic, and biochemical study of factors responsible for the flavor in peanut butter and roasted peanut. Okla. Agric. Exp. Stn., Oklahoma State Univ, Stillwater, OK.

McWatters, K.H., and J.P. Cherry. 1982. Peanut seed proteins. p. 689–736. *In* H.E. Pattee and C.T. Young (ed.) Peanut science and technology. Am. Peanut Res. Educ. Soc. Inc., Yoakum, TX.

Mercer, L.C., J.C. Wynne, and C.T. Young. 1990. Inheritance of fatty acid content in peanut oil. Peanut Sci. 17:17–21.

Moore, K.M., and D.A. Knauft. 1989. The inheritance of high oleic acid in peanut. J. Hered. 80:252–253.

Mortreuil, J.C. 1993. Une nouvelle variete d'arachide pour l'Afrique: Fleur 11. Oléagineux 48:99–102.

Norden, A.J., D.W. Gorbet, D.A. Knauft, and C.T. Young. 1987. Variability in oil quality among peanut genotypes in the Florida breeding program. Peanut Sci. 14:7–11.

O'Bryne, D.J., D.A. Knauft, and R.B. Shireman. 1997. Low fat-monounsaturated rich diets containing high-oleic peanuts improve serum lipoprotein profiles. Lipids 32:687–695.

Picket, T.A., and K.T. Holley. 1951. Susceptibility of type of peanut to rancidity development. Am. Oil Chem. Soc. 28:478–479.

Renaud S., M. De Lorgeril, J. Delaye, J. Guidollet, F. Jacquard, N. Mamelle, J.L. Martin, I. Monjaud, P. Salen, and P. Toubol. 1995. Cretan Mediterranean diet for prevention of coronary heart disease. Am. J. Clin. Nutr. 61:1360s–1367s.

Robertson, J.A., and J.K. Thomas. 1976. Chemical and microbial changes in dehulled confectionary sunflower kernels during storage under controlled conditions. J. Milk Food Technol. 39:18–23.

Sanders, T.H. 1980a. Effects of variety and maturity on lipid class composition of peanut oil. J. Am. Oil Chem. Soc. 57:8–11.

Sanders, T.H. 1980b. Fatty acid composition of lipid classes in oils from peanut differing in variety and maturity J. Am. Oil Chem. Soc. 57:12–15.

Simpson, C.E., 1972. Registration of Starr peanut. Crop Sci. 12:395.

Smith O.D., C.E. Simpson, W.J. Grichar, and H.A. Melouk. 1991. Registration of Tamspan 90 peanut. Crop Sci. 31:1711.

Strickberger, M.W. 1976. Probability and statistical testing. p. 140–201. *In* M.W. Strickberger (ed.) Genetics. Macmillan Publishing Co., Inc., New York.

Tai, Y.P. 1972. Inheritance of oleic to linoleic fatty acid ratio in peanut, *Arachis hypogaea* L. Ph.D. thesis (Diss. Abstr. AAT 7315269), Okla. State Univ., Stillwater, OK.

Tai, Y.P., and C.T. Young. 1975. Genetic studies of peanut proteins and oils. J. Am. Oil Chem. Soc. 52:377–385.

Williams, E.J., and J.S. Drexler. 1981. A non-destructive method for determining peanut pod maturity. Peanut Sci. 8:134–141.