Genotype-by-Environment Interactions for Seed Composition Traits of Breeding Lines in the Uniform Peanut Performance Test

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ABSTRACT

Peanut composition is influenced by several groups of factors: environmental, genetic, and their interaction. This study evaluated the relative contributions of these factors using data from the USDA-ARS quality testing program using samples from the multi-state Uniform Peanut Performance Tests (UPPT). Data were subjected to restricted maximum likelihood estimation of variance components reflecting the main effects of year, production region, location within region, genotype (cultivar or breeding line), and kernel grade ("seed size") within genotype, and the interactions among these main effects. Genetic variation in oil content was low (9% of total variation); however, fatty acid composition of the oil was highly influenced by genotype (34–77%) with the exception of lignoceric acid (1%). Genetic influence on tocopherols was generally less than that of fatty acids. Environmental variation of tocopherols was greater than the variation attributable to genotype-by-environment interaction. The lowest genetic variation was observed in sugar content; however, environmental variation was high (68%). The magnitude of genetic influence on oil content and fatty acid concentrations suggests that these traits are amenable to improvement through breeding.

Key Words: *Arachis hypogaea* L., fatty acid, tocopherol, oil content, O/L values, iodine value, sugars, repeatability, variance components, cultivars, breeding lines.

Flavor and texture are the aspects of sensory quality most often mentioned as important by processors of peanut (*Arachis hypogaea* L.) in the USA. Manufacturers of peanut products desire to deliver products with consistent flavor and texture. Composition influences the flavor and texture of roasted peanuts and peanut products (Ahmed and Young, 1982; Ahmed and Ali, 1986). Therefore, development of peanut cultivars whose seed composition profiles do not vary greatly from those of existing cultivars is desirable. However, peanut composition is influenced by several groups of factors including environmental factors (associated with years, production regions, locations within regions, and interactions of region and location with year), genetic factors (cultivars or breeding lines), and interaction between environmental and genetic factors (genotype-by-environment or "GxE" interaction) (Tai and Young, 1975; Layrisse *et al.*, 1980; Yadava *et al.*, 1980; Ali and Prasada Rao, 1982; Sykes and Michaels, 1986; Raheja *et al.*, 1987; Branch *et al.*, 1990; Grosso *et al.*, 1994; Harch *et al.*, 1995; Hammond *et al.*, 1997; Ku *et al.*, 1998; Upadhyaya and Nigam, 1999; Dwivedi *et al.*, 2000; Andersen and Gorbet, 2002). In order to ascertain reasonable goals with respect to consistency of seed composition of peanuts, one must know the relative contributions of genotype, environment, and GxE interaction to seed composition.

In 2002, the USDA, Agricultural Research Service, Market Quality and Handling Research Unit in Raleigh, NC (USDA, ARS, MQHRU) implemented a program to evaluate sensory quality and composition of peanuts grown in the Uniform Peanut Performance Test (UPPT) (Branch *et al.*, 2006). The UPPT is a collaborative program in which advanced breeding lines developed by the several public-sector peanut breeding programs are evaluated for agronomic performance and grade across the three US peanut-producing regions. Beginning in 2002, USDA-ARS personnel applied standard composition evaluation procedures to samples of UPPT entries from each test site, measuring oil content, fatty acid profile of seed oil, and contents of various tocopherols and sugars. The UPPT data set provides a unique opportunity to examine the contributions of genotype, environment, and GxE interaction to variation in seed composition. Each year's UPPT includes 13 to 16 breeding lines and cultivars evaluated at each of 9 locations across 7 states. UPPT breeding line entries generally do not remain in the test for more than two years, but the standard cultivars Florunner and NC 7 are included in all years, providing some across-year orthogonality. Within years, there is perfect orthogonality. The objective of this

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Table 1. Variance component estimates for oil content and quality indicators for oil extracted from graded samples from the 2002–2005 Uniform Peanut Performance Test.

Source	Oil content		Oleic-to-linoleic (O/L) ratio		Iodine value		Total saturated (16:0+ 18:0+ 20:0+ 22:0+ 24:0)		Poly-unsaturated-to-saturated (P/S) ratio		Long-chain saturated (20:0+ 22:0+ 24:0)	
	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
	%				%		%				%	
Year	1.405±1.165	17.5	0.110±0.166	0.1	0.090±0.151	0.1	0.215±0.272	1.9	0.000±0.000	0.0	0.080±0.153	1.4
Region	1.666±1.974	20.8	1.541±1.932	1.4	4.465±5.255	5.9	0.261±0.374	2.3	0.017±0.020	4.8	–	–
Year × region	0.084±0.272	1.0	–	–	0.071±0.157	0.1	0.140±0.215	1.2	–	–	0.111±0.171	1.9
Location in region	0.531±0.462	6.6	0.632±0.586	0.6	1.963±1.207†	2.6	0.120±0.153	1.1	0.007±0.004†	2.0	0.079±0.103	1.4
Year × location in region	1.184±0.354**	14.8	–	–	0.113±0.143	0.2	0.222±0.235	2.0	0.000±0.001	0.1	0.099±0.208	1.7
Genotype	0.718±0.501†	9.0	86.841±30.432**	77.5	57.282±19.753**	76.1	5.553±1.928**	49.0	0.283±0.098**	78.3	0.887±0.395*	15.5
Year × genotype	–	–	–	–	–	–	–	–	–	–	0.040±0.155	0.7
Region × genotype	0.359±0.138**	4.5	–	–	1.172±0.859†	1.6	0.076±0.218	0.7	0.002±0.003	0.6	0.034±0.212	0.6
Year × region × genotype	0.095±0.103	1.2	–	–	0.332±0.231†	0.4	–	–	0.001±0.001	0.4	–	–
Location × entry in region	0.174±0.073**	2.2	5.031±1.048**	4.5	1.135±0.330**	1.5	0.131±0.507	1.2	0.005±0.002**	1.4	0.119±0.498	2.1
Year × location × genotype in region	–	–	3.662±0.646**	3.3	1.049±0.451*	1.4	3.613±0.564**	31.9	0.006±0.002**	1.7	3.805±0.548**	66.4
Size in genotype	0.775±0.362*	9.7	9.167±4.051*	8.2	3.601±2.234†	4.8	0.155±0.178	1.4	0.021±0.012*	5.8	0.072±0.051†	1.3
Year × size in genotype	0.168±0.096*	2.1	0.236±0.311	0.2	0.018±0.135	0.0	0.038±0.154	0.3	0.001±0.001	0.2	–	–
Region × size in genotype	–	–	1.987±0.963*	1.8	2.021±1.026*	2.7	–	–	0.009±0.005*	2.6	–	–
Year × region × size in genotype	0.035±0.116	0.4	–	–	–	–	–	–	–	–	–	–
Location × size in region and genotype	–	–	–	–	–	–	–	–	–	–	–	–
Residual	0.817±0.080**	10.2	2.836±0.419**	2.5	1.931±0.371**	2.6	0.801±0.138**	7.1	0.009±0.002**	2.4	0.409±0.061**	7.1
Environmental		60.8		2.0		8.9		8.5		6.8		6.4
Genetic		9.0		77.5		76.1		49.0		78.3		15.5
GxE		7.8		7.8		4.9		33.7		4.0		69.7
Kernel size		9.7		8.2		4.8		1.4		5.8		1.3
Size × environment		2.5		2.0		2.7		0.3		2.7		0.0
Residual		10.2		2.5		2.6		7.1		2.4		7.1
Repeatability of a single observation	0.090		0.775		0.761		0.490		0.783		0.155	
Repeatability of a mean across all locations and regions in one year	0.175		0.872		0.881		0.833		0.883		0.545	
Repeatability of a mean across all locations and regions in two years	0.226		0.880		0.889		0.888		0.891		0.677	

†,*,** Denote variance components significantly greater than zero at P<0.10, P<0.05, and P<0.01, respectively, by z-test.

Table 2. Variance component estimates for medium-chain fatty acid composition of oil extracted from graded samples from the 2002–2005 Uniform Peanut Performance Test.

Source	Palmitic (16:0)		Stearic (18:0)		Oleic (18:1)		Linoleic (18:2)	
	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
	%							
Year	0.267±0.283	7.6	0.025±0.037	3.8	0.620±1.141	0.3	0.429±0.768	0.3
Region	–	–	0.142±0.158	21.0	4.046±5.829	2.0	5.333±6.860	3.4
Year × region	0.029±0.026	0.8	0.002±0.019	0.4	1.053±0.912	0.5	0.696±0.617	0.4
Location in region	0.017±0.015	0.5	0.001±0.016	0.2	1.168±0.920	0.6	1.383±1.010†	1.0
Year × location in region	0.002±0.010	0.1	0.055±0.024*	8.2	–	–	–	–
Genotype	2.240±1.069*	63.3	0.226±0.116*	33.6	135.670±66.067*	66.9	101.200±49.910*	64.6
Year × genotype	0.006±0.017	0.2	0.010±0.011	1.4	0.076±0.255	0.0	–	–
Region × genotype	0.053±0.077	1.5	0.076±0.032**	11.2	0.520±4.000	0.3	0.887±3.231	0.6
Year × region × genotype	0.023±0.024	0.7	0.015±0.012	2.3	–	–	–	–
Location × entry in region	0.025±0.038	0.7	0.035±0.009**	5.2	3.152±1.057**	1.6	2.996±0.888**	1.9
Year × location × genotype in region	0.134±0.033**	3.8	0.019±0.007**	2.8	4.315±0.696**	2.1	3.298±0.485**	2.1
Size in genotype	0.472±0.318†	13.3	0.024±0.021	3.6	36.085±21.793*	17.8	27.988±16.975*	17.9
Year × size in genotype	–	–	0.001±0.008	0.2	–	–	–	–
Region × size in genotype	0.223±0.099*	6.3	0.011±0.010	1.6	15.513±5.654**	7.6	11.957±4.390**	7.6
Year × region × size in genotype	–	–	0.010±0.011	1.5	–	–	–	–
Location × size in region and genotype	0.012±0.031	0.3	–	–	–	–	–	–
Residual	0.034±0.021†	1.0	0.020±0.005**	3.0	0.582±0.183**	0.3	0.373±0.115**	0.2
Environmental		9.0		33.6		3.4		5.1
Genetic		63.3		33.6		66.9		64.6
GxE		6.8		22.9		4.0		4.6
Kernel size		13.3		3.6		17.8		17.9
Size × environment		6.6		3.3		7.6		7.6
Residual		1.0		3.0		0.3		0.2
Repeatability of a single observation	0.633		0.336		0.669		0.646	
Repeatability of a mean across all locations and regions in one year	0.702		0.579		0.731		0.719	
Repeatability of a mean across all locations and regions in two years	0.746		0.627		0.744		0.732	

†,*,** Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.

Table 3. Variance component estimates for long-chain fatty acid composition of oil extracted from graded samples from the 2002–2005 Uniform Peanut Performance Test.

	Arachidic (20:0)		Gadoleic (20:1)		Behenic (22:0)		Lignoceric (24:0)	
Source	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
				%				
Year	0.009±0.010	8.2	–	–	–	–	0.114±0.227	1.5
Region	0.015±0.017	14.5	0.020±0.023	15.7	0.000±0.013	0.0	–	–
Year × region	–	–	0.000±0.001	0.1	–	–	–	–
Location in region	–	–	0.007±0.005†	5.8	0.014±0.014	2.2	0.016±0.149	0.2
Year × location in region	0.006±0.002**	5.8	0.003±0.001*	2.1	0.017±0.008*	2.9	–	–
Genotype	0.050±0.023*	47.4	0.052±0.029*	41.8	0.471±0.206*	77.2	0.065±0.218	0.8
Year × genotype	0.003±0.002*	3.0	–	–	0.005±0.005	0.9	–	–
Region × genotype	0.008±0.004*	7.2	0.001±0.003	0.9	–	–	–	–
Year × region × genotype	0.001±0.001	0.6	0.001±0.001†	0.9	–	–	–	–
Location × entry in region	0.005±0.001**	4.7	0.001±0.001*	1.2	–	–	0.046±0.867	0.6
Year × location × genotype in region	0.002±0.001*	2.2	0.003±0.001**	2.7	0.016±0.007**	2.6	7.546±1.058**	96.7
Size in genotype	–	–	0.027±0.014*	21.3	0.051±0.027*	8.3	0.009±0.007†	0.1
Year × size in genotype	–	–	0.000±0.000	0.4	0.003±0.005	0.5	0.002±0.002	0.0
Region × size in genotype	0.002±0.001†	2.0	0.007±0.003*	5.4	–	–	–	–
Year × region × size in genotype	0.001±0.001	1.1	–	–	–	–	–	–
Location × size in region and genotype	–	–	–	–	–	–	0.003±0.002*	0.0
Residual	0.003±0.001**	3.3	0.002±0.001**	1.6	0.033±0.007**	5.4	0.002±0.001*	0.0
Environmental		28.5		23.8		5.1		1.7
Genetic		47.4		41.8		77.2		0.8
GxE		17.7		5.7		3.5		97.3
Kernel size		0.0		21.3		8.3		0.1
Size × environment		3.1		5.8		0.5		0.1
Residual		3.3		1.6		5.4		0.0
Repeatability of a single observation	0.475		0.418		0.772		0.008	
Repeatability of a mean across all locations and regions in one year	0.682		0.561		0.874		0.062	
Repeatability of a mean across all locations and regions in two years	0.757		0.573		0.887		0.116	

†,*,** Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.

Table 4. Variance component estimates for tocopherol content of oil extracted from graded samples from the 2002–2005 Uniform Peanut Performance Test.

Source	α-Tocopherol		β-Tocopherol		γ-Tocopherol		δ-Tocopherol		Total tocopherol	
	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
	ug/g FW		*ug/g FW*		*ug/g FW*		*ug/g FW*		*ug/g FW*	
Year	36.81±42.27	10.3	–	–	23.17±45.65	5.4	0.38±0.44	4.1	–	–
Region	–	–	–	–	4.07±32.51	0.9	1.65±2.22	17.9	–	–
Year × region	12.52±15.43	3.5	0.01±0.05	1.4	60.19±48.07	14.0	–	–	98.10±58.77*	11.1
Location in region	4.08±9.86	1.1	0.07±0.08	7.8	15.00±19.34	3.5	1.33±0.96†	14.4	62.00±50.15	7.0
Year × location in region	46.43±16.68**	12.9	0.29±0.10**	31.5	62.89±22.63**	14.6	1.24±0.38**	13.5	135.08±41.61**	15.2
Genotype	144.18±64.46*	40.2	0.18±0.08*	19.2	161.66±61.53**	37.6	3.16±1.11**	34.3	379.39±134.25**	42.9
Year × genotype	14.18±7.77*	3.9	0.01±0.01	0.8	–	–	–	–	30.31±18.91†	3.4
Region × genotype	–	–	0.01±0.01	0.7	2.63±11.16	0.6	0.14±0.21	1.5	–	–
Year × region × genotype	10.78±4.30**	3.0	–	–	14.30±6.25*	3.3	0.11±0.07†	1.2	28.36±11.30**	3.2
Location × entry in region	0.18±6.52	0.1	–	–	16.27±4.82**	3.8	0.36±0.16*	3.8	19.83±7.92**	2.2
Year × location × genotype in region	4.31±6.94	1.2	0.01±0.03	1.1	7.89±8.73	1.8	0.00±0.10	0.0	1.25±17.92	0.1
Size in genotype	43.93±20.82*	12.2	0.03±0.04	3.5	12.02±10.26	2.8	–	–	6.50±10.44	0.7
Year × size in genotype	–	–	–	–	6.33±4.60†	1.5	–	–	5.52±11.44	0.6
Region × size in genotype	–	–	–	–	8.55±8.50	2.0	0.18±0.15	2.0	2.68±7.11	0.3
Year × region × size in genotype	–	–	–	–	–	–	–	–	–	–
Location × size in region and genotype	5.33±7.10	1.5	0.04±0.02*	4.2	–	–	0.01±0.14	0.1	–	–
Residual	36.21±6.99**	10.1	0.28±0.04**	29.8	36.41±7.69**	8.4	0.67±0.11**	7.2	116.83±17.83**	13.2
Environmental		27.8		40.7		38.3		49.9		33.3
Genetic		40.2		19.2		37.6		34.3		42.9
GxE		8.2		2.6		9.5		6.5		9.0
Kernel size		12.2		3.5		2.8		0.0		0.7
Size × environment		1.5		4.2		3.4		2.1		0.9
Residual		10.1		29.8		8.4		7.2		13.2
Repeatability of a single observation	0.4017		0.1922		0.3748		0.3428		0.4283	
Repeatability of a mean across all locations and regions in one year	0.5597		0.5927		0.6432		0.6733		0.7544	
Repeatability of a mean across all locations and regions in two years	0.6463		0.6838		0.7457		0.7268		0.8443	

†,*,** Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.

Table 5. Variance component estimates for sugar content of graded samples from the 2002–2005 Uniform Peanut Performance Test.

	Inositol		Glucose		Fructose	
Source	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
Year	–	–	90±162	1.1	235±230	4.5
Region	–	–	–	–	–	–
Year × region	540±1225	1.7	–	–	38±110	0.7
Location in region	1702±1735	5.4	–	–	82±110	1.6
Year × location in region	5364±2121**	17.1	537±264*	7.2	149±163	2.9
Genotype	358±1139	1.1	201±162	2.7	70±166	1.4
Year × genotype	–	–	–	–	–	–
Region × genotype	–	–	58±152	0.8	–	–
Year × region × genotype	–	–	–	–	–	–
Location × entry in region	1937±1356†	6.2	–	–	–	–
Year × location × genotype in region	14418±1658**	45.8	–	–	1509±593**	29.1
Size in genotype	2117±1021*	6.7	–	–	62±164	1.2
Year × size in genotype	473±479	1.5	–	–	81±154	1.6
Region × size in genotype	351±473	1.1	–	–	–	–
Year × region × size in genotype	–	–	–	–	110±214	2.1
Location × size in region and genotype	972±949	3.1	–	–	394±285†	7.6
Residual	3223±596**	10.3	6618±441**	88.2	2449±588**	47.3
Environmental		24.2		8.3		9.7
Genetic		1.1		2.7		1.4
GxE		52.0		0.8		29.1
Kernel size		6.7		0.0		1.2
Size × environment		5.7		0.0		11.3
Residual		10.3		88.2		47.3
Repeatability of a single observation	0.0114		0.0268		0.0135	
Repeatability of a mean across all locations and regions in one year	0.0557		0.1817		0.0694	
Repeatability of a mean across all locations and regions in two years	0.0760		0.3031		0.1217	

† ,*,** Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.

study was to use published UPPT results to estimate variance components associated with environmental, genotypic, and GxE effects on seed composition traits of peanuts.

Materials and Methods

Methodology used by USDA, ARS, MQHRU has been published in annual reports available online (USDA, 2003). The data from the UPPT include seed composition traits measured on bulk samples from the replicate plots grown at each of nine test locations (Suffolk, VA and Lewiston, NC in the Virginia-Carolina production area; Tifton, GA, Marianna, FL, and Headland, AL in the Southeastern production area; and Denver City, TX, Pearsall, TX, Stephenville, TX, and Fort Cobb, OK in the Southwestern production area). Growing conditions at the specific locations are described in the annual reports of yield and grade of UPPT entries (Branch *et al.*, 2003, 2004, 2005, 2006). Processing of the shelled peanuts at the USDA, ARS, National Peanut Research Laboratory resulted in samples separated into medium and jumbo grade size fractions ("sizes") for runner market types. Whenever possible, both fractions were subjected to analysis of composition. For virginia market type entries, only the extra large kernel fraction was analyzed. During the period of the study, a total of 40 breeding lines and cultivars were evaluated in the UPPT, of which 16 exhibited the high oleic fatty acid trait (Norden *et al.*, 1987; Moore and Knauft, 1989; Knauft, *et al.*, 1993).

Data from the 2002 through 2005 crop years were used in the analysis. The mixed models procedure (PROC MIXED) of the SAS statistical software package (SAS Inst., Cary, NC) was used to apply restricted maximum likelihood (REML) estimation of variance components associated with year, production region, year-by-region interaction, location within regions, year-by-location interaction in region, genotype, year-by-genotype

Table 5. Extended.

Sucrose		Raffinose		Stachyose		Total sugar	
Variance compo- ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total	Variance component ±SE	% of total
3510965±6101807	6.7	–	–	91504±94764	4.2	4187752±6744319	6.1
3102779±7794352	5.9	–	–	509714±704907	23.6	6919860±13148996	10.0
6949986±6693110	13.3	–	–	22147±60115	1.0	6217181±6700039	9.0
6968658±5838662	13.3	5080±4595	8.5	529786±334299†	24.5	12058585±8986720†	17.5
15297595±4660537**	29.3	17030±4440**	28.4	223231±72140**	10.3	17301888±5307798**	25.0
244264±1519830	0.5	6694±4352†	11.2	256131±112888*	11.9	365594±2103496	0.5
–	–	110±487	0.2	5711±15510	0.3	953136±1689927	1.4
665587±484311†	1.3	5615±2310**	9.4	28223±34384	1.3	975932±638811†	1.4
320427±725151	0.6	–	–	32369±22578†	1.5	60237±915247	0.1
–	–	3203±1190**	5.3	98239±28838**	4.5	–	–
13485±1109691	0.0	–	–	–	–	–	–
3980797±1795629*	7.6	3994±2360*	6.7	48408±33678†	2.2	5055474±2338391*	7.3
–	–	–	–	0±0	0.0	0.0	–
–	–	1321±1381	2.2	12297±23488	0.6	–	–
–	–	–	–	–	–	–	–
0±0	0.0	–	–	–	–	0±0	0.0
11177370±1229587**	21.4	16967±1356**	28.3	304082±26798**	14.1	15000306±1243714**	21.7
	68.6		36.8		63.6		67.6
	0.5		11.2		11.9		0.5
	1.9		14.9		7.6		2.9
	7.6		6.7		2.2		7.3
	0.0		2.2		0.6		0.0
	21.4		28.3		14.1		21.7
0.0047		0.1115		0.1185		0.0053	
0.0161		0.3668		0.3481		0.0181	
0.0228		0.4162		0.3960		0.0247	

interaction, region-by-genotype interaction, year-by-region-by-genotype interaction, location-by-genotype interaction in region, year-by-location-by-genotype interaction in region, kernel grade (jumbo or medium) within genotype, year-by-grade interaction in genotype, region-by-grade interaction in genotype, year-by-region-by-grade interaction in genotype, location-by-grade interaction in region and genotype. All of these effects were considered random in order to estimate a variance component. All other effects were pooled as a residual effect.

Repeatability coefficients were estimated as indicators of the magnitude of the genetic component of variance relative to the variance among genotype means estimated from one or two years in the UPPT trials. The estimates were obtained as

$$R = \frac{\hat{\sigma}^2_{G}}{\hat{\sigma}^2_{G} + \hat{\sigma}^2_{E} + \hat{\sigma}^2_{GE} + \hat{\sigma}^2_{S(G)} + \hat{\sigma}^2_{SE(G)} + \frac{\hat{\sigma}^2}{n}}$$

where $\hat{\sigma}^2_{G}$ is the variance attributable to genotypes,

$$\hat{\sigma}^2_{E} = \frac{\hat{\sigma}^2_{Y}}{y} + \frac{\hat{\sigma}^2_{R}}{r} + \frac{\hat{\sigma}^2_{YR}}{yr} + \frac{\hat{\sigma}^2_{L(R)}}{l} + \frac{\hat{\sigma}^2_{YL(R)}}{yl}$$

is the estimate of variance attributable to environments,

$$\hat{\sigma}^2_{GE} = \frac{\hat{\sigma}^2_{YG}}{y} + \frac{\hat{\sigma}^2_{RG}}{r} + \frac{\hat{\sigma}^2_{YRG}}{yr} + \frac{\hat{\sigma}^2_{LG(R)}}{l} + \frac{\hat{\sigma}^2_{YLG(R)}}{yl}$$

is the estimate of variance attributable to GxE interaction,

$$\hat{\sigma}^2_{SE(G)} = \frac{\hat{\sigma}^2_{YS(G)}}{y} + \frac{\hat{\sigma}^2_{RS(G)}}{r} + \frac{\hat{\sigma}^2_{YRS(G)}}{yr} + \frac{\hat{\sigma}^2_{LS(RG)}}{l} + \frac{\hat{\sigma}^2_{YLS(RG)}}{yl}$$

is the estimate of variance attributable to interaction between environments and grade sizes, and $\hat{\sigma}^2_{G}$, $\hat{\sigma}^2_{Y}$, $\hat{\sigma}^2_{R}$, $\hat{\sigma}^2_{YR}$, $\hat{\sigma}^2_{L(R)}$, $\hat{\sigma}^2_{YL(R)}$, $\hat{\sigma}^2_{YG}$, $\hat{\sigma}^2_{RG}$, $\hat{\sigma}^2_{YRG}$, $\hat{\sigma}^2_{LG(R)}$, $\hat{\sigma}^2_{YLG(R)}$, $\hat{\sigma}^2_{S(G)}$, $\hat{\sigma}^2_{YS(G)}$, $\hat{\sigma}^2_{RS(G)}$, $\hat{\sigma}^2_{YRS(G)}$, $\hat{\sigma}^2_{LS(RG)}$, $\hat{\sigma}^2_{YLS(RG)}$, and $\hat{\sigma}^2$ are the estimates of variances attributable to genotypes; years; regions; year-by-region interaction; locations within regions; interaction of years with locations within regions; year-by-genotype interaction; region-by-genotype interaction; year-by-region-by-genotype interaction; interaction between genotypes and locations within regions; interaction among years, genotypes, and locations within regions; seed grades within genotypes; interaction of years with seed grades within genotypes; interaction of regions with seed grades within genotypes; interaction among years, regions, and seed grades within genotypes; interaction of locations within regions with seed grades within genotypes; and interaction among years, locations within regions, and seed grades within genotypes; and residual effects (experimental error). For purposes of estimation, the number of years (y) was either 1 or 2, the number of regions (r) was 3, the total number of locations (l) was 9, and the number of kernel grades measured per genotype was 1.

Results and Discussion

Because of their influence on processing quality and shelf life, oil content and fatty acid concentrations are among the most important seed composition traits (Ahmed and Young, 1982; Sanders *et al.*, 1995). Very little genetic variation in measured oil content was noted among the samples, approximately 9% of the total variation (Table 1). In the current study, UPPT entries were either runner or virginia market types, perhaps constraining genetic variance, while the environmental representation was wide. Greater genetic variation might have been observed had there been UPPT entries of the spanish or valencia market types. Environmental effects accounted for 61% of the total variation for oil content, GxE effects only 8%, and seed grade (size) within genotype 10%, slightly more than the amount due to genotypes. Almost all of the variation in size was the result of runner-type breeding lines producing appreciable amounts of jumbo and medium kernels. Jumbo runner kernels generally had higher oil content than medium runner kernels.

In contrast to oil content, most measures of oil quality were strongly influenced by genotype (Table 1), especially the traits that reflected the difference in oleic and linoleic fatty acids conditioned by the high-oleic seed oil trait identified by researchers at the Univ. of Florida (Norden *et al.*, 1987; Moore and Knauft, 1989, Knauft *et al.*, 1993). The high-oleic trait influenced not only the contents of oleic and linoleic fatty acids (67% and 65% genotypic relative to total variation, respectively), but also palmitic (63%) and stearic (34%) acids (Table 2) as well as long-chain species arachidic (48%), gadoleic (42%), and behenic (77%) fatty acids (Table 3). These effects on specific fatty acids resulted in similarly large genotypic influence in oleic-to-linoleic ratio (78%), iodine value (76%), total saturates (49%), and ratio of polyunsaturates to saturates (78%) (Table 1). Similar genotypic responses of oil quality indicators were not unexpected; the pleiotropic effects of the genes that cause the high-oleic trait in peanut have been reported previously (Isleib *et al.*, 2006). The only fatty acid that was not strongly influenced by genetics was lignoceric acid for which 97% of total variation was attributed to GxE interaction arising from specific combinations of genotypes, years, and individual locations within regions (Table 3). Lack of genetic variation in this fatty acid is also reflected in the limited genetic variation value of long-chain saturated fatty acids (15%) (Table 1).

Tocopherols were generally less influenced by genetics than were fatty acids as exemplified by the repeatability of a single observation which ranged from 19% to 42% (Table 4). However, compared with pod yield (data not shown), this range of repeatability would be considered high. Environmental variation in concentration of the four tocopherols and for total tocopherol was greater than variation attributable to GxE. The relative contents of the tocopherol forms were associated with the high-oleic acid trait. High-oleic lines contained less α- (93.6 vs. 99.5 ug/gFW, $P<0.01$) and β-tocopherols (3.3 vs. 3.5 ug/gFW, $P<0.01$) and more γ- (92.6 vs. 85.2 ug/gFW, $P<0.01$) and δ-tocopherol (6.0 vs. 5.8 ug/gFW, $P<0.10$), although the total tocopherol content was not different (191.2 vs. 195.7 ug/gFW, NS)

In contrast to oil and tocopherol contents and fatty acid concentrations, genetic variation for sugar concentrations was low (Table 5). There was a preponderance of environmental variation for concentrations of sucrose (69% of total variation), raffinose (37%), stachyose (64%), and total sugars (68%). Sucrose comprises the majority of the total sugars in peanut seeds, explaining the similar findings for sucrose and total sugars. Interaction between years and locations within production regions was the largest single environmental factor influencing sucrose and total sugar concentrations. Although they make up only a small part of total sugars, genotypic variability of raffinose and stachyose was 11.2% and 11.9% of total variation, respectively. Variation due to GxE effects was the largest part of total variation for inositol (52% of total variation) and was mostly associated with specific combinations of year, location, and genotype within production regions. The largest contributor to variation for glucose and fructose concentrations was residual error associated with specific samples.

The magnitude of genetic influence on oil content and fatty acid concentrations suggests that these traits are amenable to genetic improvement. Development of cultivars with the high-oleic seed oil trait is already a common feature of all U.S.-based peanut breeding programs. With the recent public interest in biofuels, genetic improvement of oil content may also become a common breeding objective. Alteration of tocopherol profiles also appears to be feasible based on the magnitude of genetic relative to total variation. Low genetic variation of total sugar content suggests that its modification would be challenging. However, modification of raffinose and/or stachyose may be feasible. As was the case for sensory quality (Isleib *et al.*, 2008), environmental influence on total sugar content of peanut begs the question of which specific environmental factors produce the variation. The importance of specific combinations of locations, years, and production regions suggests highly localized factors.

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