Genotype-by-Environment Interactions for Flavor Attributes of Breeding Lines in the Uniform Peanut Performance Test

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ABSTRACT

Peanut flavor is influenced by several groups of factors: environmental, genetic, and interaction between them. This study evaluated the relative contributions of these factors using data from the USDA-ARS program of sensory quality testing of 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 regions, genotype, and kernel grade within genotype, and the interactions among these main effects. Genetic variation was relatively small (0.0 to 9.5% of total variation) while environmental variation, particularly that due to years, was large. Year-by-genotype interaction was large for roast color and intensities of the roasted peanut and sweet aromatic attributes. Estimates of repeatability (R) for sensory attributes were low, even based on means measured across multiple locations and two years, except for that of the sweet attribute (R = 0.10 for a single observation and R = 0.34 for a mean across two years of UPPT testing). Breeders should be able to reliably identify lines with superior sweet attribute intensity, but identification of lines with intense roasted peanut attribute will be more difficult.

Key Words: *Arachis hypogaea* L., sensory quality, repeatability, variance components, varieties.

Flavor is among the most important quality attributes for commercial acceptance of roasted peanuts (*Arachis hypogaea* L.) as snacks or peanut butter. Manufacturers of peanut products desire to deliver consistently flavorful products. Peanut breeding programs are sensitive to the need to at least maintain, but ideally improve, peanut flavor of new cultivars. However, peanut flavor is influenced by several groups of factors: environmental factors (associated with years, production regions, locations within regions, and interactions of region and location with year), genetic factors (cultivars), and interaction between environmental and genetic factors (genotype-by-environment or "G×E" interaction). In order to ascertain reasonable goals with respect to consistency of flavor of peanut products, one must know the relative contributions of genotype, environment, and G×E interaction to sensory quality.

In 2002, the USDA Agricultural Research Service (USDA-ARS) implemented a sensory quality testing program for peanuts grown as part of 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 sensory evaluation procedures to samples of UPPT entries from each test site. The UPPT flavor data set provides a unique opportunity to examine the contributions of genotype, environment, and G×E interaction to variation in sensory quality. Previous estimates of variance components, broad-sense heritabilities, and standard errors of the differences between means were based on analysis of data collected on samples donated by breeding and variety testing programs in different states (Pattee and Giesbrecht, 1990; Pattee *et al.*, 1993, 1994, 1997, 1998). Although samples of Florunner, NC 7, or a spanish or Valencia market-type check were submitted along with samples of experimental breeding lines, the data collected on donated samples suffers from a lack of orthogonality. In contrast, each year's UPPT includes 13 to 16 breeding lines and cultivars evaluated at each of 9 locations across 7 states. Within years, there is perfect orthogonality. Experimental UPPT entries generally do not stay in the test for more than two years, but the check cultivars Florunner and NC 7 are included in all years, providing greater across-year orthogonality than is found in the donated data set. The objective of this study was to use published UPPT results to estimate variance components associated with environmental, genotypic, and G×E effects on sensory quality of peanuts.

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Materials and Methods

Methodology of the USDA-ARS Market Quality and Handling Research Unit (MQHRU) at Raleigh, NC has been published in annual reports available online (Uniform Peanut Performance Tests, 2003. Chemical, Sensory and Shelf-life Properties. Data Presented by Location. July, 2003. USDA-ARS-SAA Market Quality and Handling Research Unit, Raleigh, NC, pp. 4–7, http://152.1.118.33/, validated 21 Feb 2007). The data from the UPPT include paste color and sensory attribute intensities 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 or Brownfield, TX, Stephenville, TX, Pearsall, TX, and Fort Cobb, OK in the Southwestern production area). Processing of the shelled peanuts resulted in samples separated into US medium and jumbo grade size fractions for runner types. Whenever possible, both fractions were subjected to sensory analysis. For virginia market-type entries, only the extra large kernel fraction was analyzed.

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 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 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 G×E 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 grades, 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 ("sizes") 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 seed grades (s) measured per genotype was 1.

Results and Discussion

Roasted peanut is the most important among the sensory attributes. It exhibited very little genetic variation, approximately 1% of the total (Table 1). This is substantially less than the estimated proportion (6 to 31%) published previously (Pattee *et al.*, 1990, 1993, 1995, 1998). The highest estimate

Table 1. Variance component estimates for the roasted peanut, sweet, bitter, astringent, and fruity/fermented sensory attribute intensities of processed peanut samples from the 2002–2005 Uniform Peanut Performance Test.

Source	Roasted peanut Variance component±SE (flavor intensity unit)	% of total	Sweet Variance component±SE (flavor intensity unit)	% of total	Bitter Variance component±SE (flavor intensity unit)	% of total	Astringent Variance component±SE (flavor intensity unit)	% of total	Fruity/fermented Variance component±SE (flavor intensity unit)	% of total
Year	0.1059±0.0941	23.8	0.0247±0.0197	19.1	0.1052±0.0769†	50.4	0.0057±0.0042†	36.6	0.0098±0.0168	5.1
Region	0.0051±0.0077	1.1	0.0063±0.0142	4.9	0.0059±0.0079	2.8	—		0.0114±0.0209	5.9
Year × region	—§		0.0004±0.0039	0.3	—		—		0.0092±0.0152	4.8
Location in region	—		0.0211±0.0139†	16.4	—		—		0.0092±0.0136	4.8
Year × location in region	0.0300±0.0090**	6.7	0.0125±0.0050**	9.7	0.0252±0.0072**	12.1	0.0015±0.0005**	9.9	0.0571±0.0185**	29.6
Genotype	0.0052±0.0318	1.2	0.0123±0.0062*	9.5	0.0032±0.0050	1.5	0.0000±0.0001	0.0	—	
Year × genotype	0.1980±0.0726**	44.5	0.0075±0.0059	5.8	0.0005±0.0050	0.2	—		—	
Region × genotype	0.0006±0.0031	0.1	0.0011±0.0017	0.8	—		—		0.0038±0.0030	2.0
Year × region × genotype	—		—		—		—		—	
Location × entry in region	—		—		—		—		—	
Year × location × genotype in region	—		0.0079±0.0057†	6.1	—		—		—	
Grade in genotype	—		—		0.0069±0.0053†	3.3	—		0.0042±0.0037	2.2
Year × grade in genotype	—		—		0.0007±0.0053	0.3	—		0.0054±0.0047	2.8
Region × grade in genotype	—		—		—		—		—	
Year × region × grade in genotype	—		—		—		—		0.0001±0.0052	0.0
Location × grade in region and genotype	—		—		—		—		—	
Residual	0.1004±0.0075**	22.6	0.0352±0.0055**	27.3	0.0612±0.0043**	29.3	0.0083±0.0005**	53.5	0.0826±0.0069**	42.9
Environmental	0.1409	31.7	0.0649	50.4	0.1362	65.3	0.0072	46.5	0.0966	50.2
Genetic	0.0052	1.2	0.0123	9.5	0.0032	1.5	0.0000	0.0	0.0000	0.0
G×E	0.1986	44.6	0.0164	12.7	0.0005	0.2	0.0000	0.0	0.0038	2.0
Grade	0.0000	0.0	0.0000	0.0	0.0069	3.3	0.0000	0.0	0.0042	2.2
Grade × environment	0.0000	0.0	0.0000	0.0	0.0007	0.3	0.0000	0.0	0.0055	2.8
Residual	0.1004	22.6	0.0352	27.3	0.0612	29.3	0.0083	53.5	0.0826	42.9
Repeatability of a single observation	0.0117		0.0953		0.0152		0.0001		0.0000	
Repeatability of a mean across all locations and regions in one year	0.0160		0.2211		0.0248		0.0001		0.0000	
Repeatability of a mean across all locations and regions in two years	0.0314		0.3382		0.0453		0.0002		0.0000	

†,*,**Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.
§variance components designated "—" denote effects found to be not significant in the restricted maximum likelihood estimation procedure and dropped from the linear model.

Table 2. Variance component estimates for roast color and the dark roast, raw/beany, stale/cardboard, and sweet aromatic attribute intensities of processed peanut samples from the 2002–2005 Uniform Peanut Performance Test.

Source	Roast color		Dark roast		Raw/beany		Stale/cardboard		Sweet aromatic	
	Variance component±SE	% of total	Variance component±SE	% of total	Variance compo-nent±SE	% of total	Variance component±SE	% of total	Variance component±SE	% of total
	Hunter L score		flavor intensity unit		flavor intensity unit		flavor intensity unit		flavor intensity unit	
Year	0.4639±4.2744	0.9	0.0320±0.0259	15.5	0.0203±0.0169	14.3	0.0143±0.0129	12.7	0.0217±0.0232	13.4
Region	—		—		—		—		—	
Year × region	1.0308±0.7765†	1.9	—		—		0.0062±0.0048†	5.5	—	
Location in region	0.8864±0.6232†	1.6	0.0162±0.0116†	7.9	0.0126±0.0089†	8.9	0.0048±0.0037	4.3	0.0031±0.0037	1.9
Year × location in region	1.2593±0.4744**	2.3	0.0241±0.0084**	11.7	0.0185±0.0062**	13.1	0.0049±0.0034†	4.3	0.0150±0.0048**	9.2
Genotype	—		0.0065±0.0111	3.1	—		—		0.0075±0.0138	4.6
Year × genotype	44.4276±10.6061**	82.7	—		—		—		0.0702±0.0275**	43.2
Region × genotype	—		—		0.0019±0.0031	1.3	—		0.0000±0.0017	0.0
Year × region × genotype	—		—		—		—		—	
Location × entry in region	—		—		—		—		—	
Year × location × genotype in region	0.0760±0.4505	0.1	—		—		0.0029±0.0101	2.5	0.0015±0.0024	0.9
Size in genotype	0.8827±0.8196	1.6	0.0223±0.0128*	10.8	0.0156±0.0071*	11.0	0.0164±0.0056**	14.6	—	
Year × size in genotype	1.4289±0.9783†	2.7	0.0054±0.0051	2.6	0.0059±0.0042†	4.2	—		—	
Region × size in genotype	—		—		—		—		—	
Year × region × size in genotype	—		—		—		—		—	
Location × size in region and genotype	0.0030±0.1830	0.0	—		0.0010±0.0045	0.7	—		—	
Residual	3.2711±0.4905**	6.1	0.0997±0.0069**	48.3	0.0659±0.0068**	46.6	0.0630±0.0107**	56.0	0.0436±0.0036**	26.8
Environmental	3.6404	6.8	0.0724	35.1	0.0513	36.3	0.0302	26.9	0.0398	24.5
Genetic	0.0000	0.0	0.0065	3.1	0.0000	0.0	0.0000	0.0	0.0075	4.6
G×E	44.5036	82.8	0.0000	0.0	0.0019	1.3	0.0029	2.5	0.0717	44.1
Kernel size	0.8827	1.6	0.0223	10.8	0.0156	11.0	0.0164	14.6	0.0000	0.0
Size × environment	1.4319	2.7	0.0054	2.6	0.0069	4.9	0.0000	0.0	0.0000	0.0
Residual	3.2711	6.1	0.0997	48.3	0.0659	46.6	0.0630	56.0	0.0436	26.8
Repeatability of a single observation	0.0000		0.0313		0.0000		0.0000		0.0461	
Repeatability of a mean across all locations and regions in one year	0.0000		0.0789		0.0000		0.0000		0.0704	
Repeatability of a mean across all locations and regions in two years	0.0000		0.1149		0.0000		0.0000		0.1309	

†,*,**Denote variance components significantly greater than zero at $P<0.10$, $P<0.05$, and $P<0.01$, respectively, by z-test.
§variance components designated "—" denote effects found to be not significant in the restricted maximum likelihood estimation procedure and dropped from the linear model.

was obtained from data collected only on virginia-type lines grown at two fairly close locations (Suffolk, VA and Pendleton, NC), perhaps restricting the amount of environmental and G×E variation and thereby increasing the relative proportion due to genetic variation. The lowest and most recent estimate (Pattee *et al.*, 1998) was calculated from data on samples including all four market types of peanuts and representing environments from three production regions and several years. The wider genetic representation should have maximized the genetic variance, but the greater environmental representation should have increased the environmental and G×E components. In the current study, UPPT entries were either runner or virginia market-types, perhaps constraining genetic variance, while the environmental representation was wide. Environmental effects accounted for 32% of the total variation for roasted peanut, and G×E effects 45%, almost all of it year-by-genotype (Y×G) interaction. The form of G×E effect previously found to have the largest impact on the roasted peanut attribute was between genotypes and specific locations within years and regions (Pattee *et al.*, 1998). In that study, Y×G interaction was a minor contributor to the overall G×E variation. The relatively small influence of Y×G interaction in previous studies may reflect the limited number of genotypes replicated across years in those studies. Although the number of UPPT entries retained from year to year is limited, there are almost always a few experimental lines retained for a second or greater year, and the checks Florunner and NC 7 are included every year at all locations. Therefore, the UPPT data should provide a better estimate of the Y×G component of variance than was previously available.

For the sweet attribute, genotypes accounted for the largest proportion of total variation of any sensory attribute, 9.5% (Table 1). Likewise, the relative magnitude of environmental factors (50.4% of total variation) was larger than that for roasted peanut although the absolute magnitude of the environmental variance component for sweet was approximately half that for roasted peanut. However, G×E variance was much smaller for sweet than for roasted peanut both in absolute value and relative to total variance. The sweet attribute had the greatest repeatability coefficients of any of the sensory attributes whether considering a single observation ($R = 0.10$) or means across one ($R = 0.22$) or two years ($R = 0.34$) of UPPT testing. Repeatability of two-year means for roasted peanut were estimated at only $R = 0.03$. In a practical sense, this implies that breeders should be able to

identify breeding lines with superior sweet scores with a high level of confidence based on means across one or two years of multiple-year testing, but that lines with superior roasted peanut intensity will be more difficult to identify accurately.

The bitter attribute exhibited the most environmental variation as a proportion of total of any sensory attribute even though the actual estimate of the environmental component of variance was very close to that for roasted peanut (0.1362 versus 0.1409 flavor intensity units or "fiu") (Table 1). As was the case for roasted peanut, most of the environmental variation for bitter was associated with years rather than spatial factors such as production region or location within region. There was very little G×E variation for bitter. Repeatability of estimates of bitter was very similar to that for roasted peanut.

Genetic effects accounted for only a small proportion of each of the other sensory attributes (Tables 1 and 2), ranging from 0% of total variation for the fruity/fermented, astringent, and raw/beany attributes to 4.6% of the sweet aromatic attribute. Environmental effects were a much larger source of variation for sensory quality (24.5 to 50.2% of total variation). Like the roasted peanut attribute, the sweet aromatic attribute exhibited a large effect of Y×G interaction.

Of particular note is the magnitude of environmental effects for the fruity/fermented attribute, 50% of the total, with the balance due to the effects of sample-to-sample (experimental) error. Among the environmental effects on the fruity/fermented attribute, specific combinations of years and locations within regions were the largest (30% of total variation). This sort of effect specific to a particular year at a particular location may reflect the average maturity of the peanuts at harvest, or it might reflect a problem with post-harvest handling of the pod samples from a specific UPPT trial.

Roast color exhibited no variation associated with genotypes. Given that the roasting protocol called for each sample to be roasted to a degree that would result in a common paste darkness (Hunter L score of approximately 49), one might expect there to be no variation in roast color. However, there was a small environmental influence on roast color and a substantial G×E variance (82.8% of total variation), again due primarily to Y×G effects. Roast color is often associated with the two sensory attributes dark roast and raw/beany. Peanuts roasted too light tend to have higher raw/beany intensity while peanuts roasted too dark have greater dark roast intensity. These two sensory attributes exhibit strong negative correla-

tion (data not shown), and the estimates of variance components for the two attributes in the current study mirror each other as one might expect, but they do not correlate with the variance components for roast color. Raw/beany and dark roast exhibited very little variation that could be attributed to design effects in the linear statistical model describing the UPPT trials. Almost half of the total variation was associated with random effects usually called experimental error or ''noise.''

The preponderance of environmental influence on sensory quality of peanuts raises the question of which specific environmental factors produce the variation. The relatively large effect of years on flavor suggests factors that affect the entire peanut-growing area of the U.S.A. Variation in temperature and rainfall tends to be more localized than the entire peanut-growing area, so it does not seem likely that these are the factors of interest. Other potential factors include changes in the disease and insect complexes that affect peanut growth, in the agrichemicals applied to manage diseases and pests, or other cultural practices such as planting dates, harvest dates, rotations, and drying protocols.

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