

Ancestral Contributions to Roasted Peanut Attribute¹

T.G. Isleib*², H.E. Pattee³, and F.G. Giesbrecht⁴

ABSTRACT

Estimates of broad-sense heritability for roasted flavor attribute of peanut (*Arachis hypogaea* L.) range from 9 to 24% on a single-plot basis. Response to selection is determined by the narrow-sense heritability, calculated from estimates of additive genetic variance which are not available for this trait. One way to assess the additive component of genetic variation is to determine how much of the total phenotypic variation can be predicted from genetic contributions of ancestors of the individuals measured. From 1986 to 1991, samples of 128 peanut cultivars and breeding lines were obtained from peanut research programs representing the three major production areas in the U.S. Samples were roasted to a nearly common color, ground into paste, and assessed for roasted flavor and fruity attribute by a trained sensory panel. CIELAB L* color was also measured for use as a covariate in statistical analysis to adjust for small differences in color. The sum of squares associated with the 128 genotypes accounted for 11% of the total phenotypic variation. Ancestry of the lines was traced back to 47 progenitors for which no further pedigree information was available. Eight progenitors made ancestral contributions that were linearly dependent on the other 39. Ancestral effects accounted for 53% of the genotypic variation, i.e., 6% of the phenotypic variation. Despite shortcomings of this 6% figure as an estimate of narrow-sense heritability for roasted flavor, no other estimates are extant. The residual (nonadditive) variation among genotypes after accounting for ancestral (additive) effects was highly significant. Multiple regression model-building techniques were used to identify 13 ancestors exerting significant effects on roasted flavor. Jenkins Jumbo, F231 (a cross of Dixie Giant with Small White Spanish 3x-2), and Improved Spanish 2B were the only ancestors among the 13 that were common to 40 or more of the 128 lines tested. Jenkins Jumbo was the single most important ancestor, exerting a negative effect on flavor ($b = -1.25 \pm 0.19$). Its progeny would be expected to have roast flavor scores reduced by $|b|/2 = 0.62$ units and grandprogeny by $|b|/4 = 0.31$ units. All but four of the 13 ancestors deemed important had deleterious effects on flavor.

Key Words: *Arachis hypogaea* L., breeding, additive genetic effects, roasted peanut flavor.

Flavor of roasted peanut (*Arachis hypogaea* L.) seed is an important characteristic influencing consumer acceptance, yet there has been little research into the genetic factors influencing roasted flavor. Significant variation for flavor among cultivars and breeding lines has been reported (Pattee and Giesbrecht, 1990, 1994; Pattee *et al.*, 1993). Estimates of broad-sense heritability for roasted peanut flavor range from 9.3 to 24.3% on a single-plot basis (Pattee *et al.*, 1994). Response to selection for flavor is determined not by broad-sense heritability but by the narrow-sense heritability of the trait, i.e., the ratio of additive genetic variance to total phenotypic variance. One method to assess the additive component of genetic variation is to determine how much of the total phenotypic variation can be predicted from genetic contributions of ancestors of the individuals measured. Parent-offspring regression is the simplest case of using ancestral contribution as a means of estimating narrow-sense heritability (Falconer, 1981).

In the U.S., peanuts are produced mainly in three regions: the Southeast (Georgia, Florida, and Alabama), the Southwest (Texas and Oklahoma), and the Virginia-Carolina area (Virginia and North Carolina). The three regions are differentiated not only by the prevailing environmental conditions but also by the market types of the array of cultivars used therein. Claims of superiority in flavor for one market type or another are often made, but comparisons of flavor between market types commonly are confounded with differences in the predominant production region for those types. Peanut production in the Virginia-Carolina area is exclusively the virginia market type while producers in the Southeast grow mainly runner-type peanuts. In the Southwest, runner, virginia, and spanish market types are all produced, but runner and spanish cultivars predominate.

The ancestors of cultivars in the runner and virginia market-types are predominantly members of *A. hypogaea* ssp. *hypogaea* var. *hypogaea*, but in both types there has been substantial introgression of germplasm from spanish (*A. hypogaea* ssp. *fastigiata* Waldron var. *vulgaris* Harz) ancestors (Isleib and Wynne, 1992). Because runner- and virginia-type cultivars often have been crossed in cultivar development programs, the degree of genetic relationship between virginia and runner cultivars can be considerable (Knauff and Gorbet, 1989). When the average degree of coancestry between market types is calculated using Knauff and Gorbet's individual coancestries, spanish types are less related to virginia ($\bar{r}_{sp*vi} = 0.003$) or runner types ($\bar{r}_{ru*sp} = 0.004$) than are virginia to runner types ($\bar{r}_{ru*vi} = 0.124$). The objectives

¹The research reported in this publication was a cooperative effort of the North Carolina Agric. Res. Serv. and the USDA-ARS, Raleigh, NC 27695-7643. The use of trade names in the publication does not imply endorsement by the North Carolina Agric. Res. Serv. or the USDA of the products named nor criticism of similar ones not mentioned. Partial funding was received from the North Carolina Peanut Growers Association.

²Assoc. Prof., Dept. of Crop Science, North Carolina State Univ., Box 7629, Raleigh, NC 27695-7629.

³Res. Chem., USDA-ARS, Dept. of Botany, North Carolina State Univ., Box 7625, Raleigh, NC 27695-7625.

⁴Prof., Dept. of Statistics, North Carolina State Univ., Box 8203, Raleigh, NC 27695-8203.

*Corresponding author.

of this research were (a) to determine how much of the phenotypic variation in roasted peanut flavor among genetically diverse cultivars and breeding lines could be ascribed to the effects of their ancestors and (b) to estimate the ancestral genetic contributions to roasted peanut flavor.

Materials and Methods

Genetic Resources. Seed samples were obtained from peanut breeding and cultivar testing programs in Florida, Georgia, North Carolina, Oklahoma, Texas, and Virginia. Nearly all commercially available cultivars and more than 150 breeding lines were included. Each market-type grown in the U.S. was represented in the set although virginia and runner types predominated. All samples were obtained from individual yield test plots grown and harvested under standard recommended procedures for the specific location. A total of 30 environments (year-location combinations) were represented in the data used for this study. The 1986, 1987, 1988, 1990, and 1991 crop years were represented. Samples from two programs (T.A. Coffelt, USDA-ARS, and R.W. Mozingo, Virginia Polytechnic Inst. and State Univ.) at the Tidewater Agric. Res. Stn. in Suffolk, VA, were considered to originate from different sources because different post-harvest handling procedures were used. Replicate samples for each genotype were obtained from different plots at a given location when available.

Sample Handling. Each year, a 1000-g sample of the sound-mature-kernel (SMK) fraction from each replicate of each location-entry was shipped to Raleigh, NC, in February following harvest and placed in storage at 5 C and 60% RH until roasted. Each SMK fraction was screened using standards for the market type of the individual cultivar or line.

Sample Roasting and Preparation. The peanut samples from each year were roasted between May and July using a Blue M "Power-O-Matic 60" laboratory oven, ground into a paste, and stored in glass jars at -20 C until evaluated. The roasting, grinding, and color measurement protocols were as described by Pattee and Giesbrecht (1990) and Pattee *et al.* (1991).

Sensory Evaluation. A trained eight-member sensory panel at the Food Science Dept., North Carolina State Univ., Raleigh, NC, evaluated all peanut paste samples for roasted flavor attributes using a 14-point intensity scale. Sensory evaluation commenced mid-June and continued until all samples were evaluated. Panel orientation and reference control were as described by Pattee and Giesbrecht (1990) and Pattee *et al.* (1993). Two sessions were conducted each week on nonconsecutive days. Panelists evaluated five samples per session in 1987-88, and four samples per session in subsequent years. The averages of individual panelists' scores on sensory attributes were used in all analyses.

Ancestral Contributions. Pedigree information was available for only 128 of the lines in the data set. Ancestry was traced back until no further information was available. There were 47 progenitors for the 128 genotypes used for statistical analysis; 47 variables were created reflecting the genetic contribution of the progenitors to the ancestry of a given line (Table 1). The genetic contribution of a parent to its progeny was assumed to be 1/2 in any given cross. The 47 variables summed to one for each line tested.

Statistical Analysis. The full data set (695 observa-

tions) was subjected to analysis of variance, partitioning the variation ascribable to environment, genotype, and the covariates previously found to significantly affect roasted peanut attribute, i.e., linear and quadratic effects of roasted color, and the linear effect of fruity attribute (Pattee *et al.*, 1994). Because the focus of this study was to partition the sum of squares due to genotype, the spatial (location) and temporal (year) components of environmental effects were not separated. Variation due to genotypes was further partitioned into two parts: variation ascribable to genetic contributions of the 47 progenitors ("additive" effects) and residual ("nonadditive") genetic variation. A regression model selection procedure was used to determine which ancestors had significant effects on roasted flavor. Some pairs of ancestors contributed to the lines evaluated for flavor only through a single path of descent resulting in perfect correlation of their contributions. Only one member of such pairs was used in the statistical analysis. Ancestral contributions were checked for more complex linear dependencies using multiple regression. When dependencies were detected, one member of any dependent group was removed to eliminate singularity of the ancestral contribution matrix and permit estimation of effects. A series of regression models were tested for goodness of fit starting with a minimal model including only the effects of environments and covariates. All possible combinations of up to 15 ancestors were examined. The coefficient of multiple determination (R^2) was used as the criterion for selecting the "best" regression model within a set of models of a particular size, e.g., models with seven ancestors included. The C_p statistic (Neter and Wasserman, 1974) was used as the criterion for deciding when the regression model adequately accounted for the variation. Use of the C_p criterion for model selection requires that one calculate:

$$C_p = \frac{SSE_p}{\hat{\sigma}^2} - (n-2P) \quad [\text{Eq. 1}]$$

where SSE_p is the error sum of squares from the model with p parameters (including the intercept), $\hat{\sigma}^2$ is the estimate of experimental error from the full model, and n is the number of observations. Models that account for the observed variation adequately produce C_p values close to p . Because of the high level of significance of the residual genotypic sum of squares left after accounting for all ancestral contributions, the residual sum of squares was added to the sum of squares due to regression on the subset of ancestors in calculation of C_p , and the 88 degrees of freedom associated with the residual were included in the number of parameters for the model. Regression coefficients were estimated for the ancestors included in the final model selected. SAS procedures GLM and REGR were used for all statistical analyses (SAS Institute, Inc., 1990).

Results and Discussion

Of the 47 ancestors contributing to the 128 lines asayed for roasted peanut flavor, only seven (Basse, Dixie Giant, Jenkins Jumbo, NC 4, Small White Spanish 3x-2, Spanish 18-38, and Improved Spanish 2B) appeared in at least one quarter of the 128 pedigrees (Table 1). These lines accounted for nearly half (48%) of the ancestral contributions in the 128 lines. Dixie Giant, Jenkins Jumbo, and Small White Spanish 3x-2 alone accounted for 32% of the total ancestry of the 128 lines. Seventeen

Table 1. Ancestral lines contributing to gene pool of 128 cultivars and breeding lines assayed for roasted peanut flavor, number of assayed lines in which the ancestors appeared, average contribution to the 128 cultivars, and average, minimum, and maximum contributions to cultivars and lines descended from the ancestors.

Code	Ancestor	Frequency in assayed lines	Avg contribution to 128 entries	Contribution to descendants			Std. dev.
				Average	Minimum	Maximum	
X ₁	<i>Arachis monticola</i>	3	0.4	16.7	12.5	25.0	7.2
X ₂	Argentine	5	2.0	51.3	6.3	100.0	33.2
X ₃	Atkin's Runner	7	1.6	28.6	6.3	50.0	21.0
X ₄	Basse ^{1a}	92	6.4	9.0	0.8	25.0	4.3
X ₅	Chalimbana	1	0.4	50.0	50.0	50.0	-
X ₆	Chico	8	3.5	56.3	25.0	100.0	29.1
X ₇	Dixie Giant ²	91	12.4	17.4	3.1	37.5	7.6
X ₈	Dixie Spanish	1	0.1	12.5	12.5	12.5	-
X ₉	Holland Station Jumbo	19	1.6	10.5	3.1	12.5	3.5
X ₁₁	Jenkins Jumbo	74	9.2	15.9	3.1	100.0	12.7
X ₁₂	Krinkle Leaf ³	13	4.8	47.1	12.5	50.0	10.4
X ₁₃	Makulu Red	1	0.2	25.0	25.0	25.0	-
X ₁₆	McSpan Spanish ^{2,4}	24	0.3	1.4	0.4	2.3	0.5
X ₁₇	NC 4	35	2.0	7.3	3.1	12.5	3.1
X ₁₈	NC Bunch	28	2.0	9.3	3.1	25.0	6.4
X ₁₉	NC Runner ^{2,4}	1	0.0	3.1	3.1	3.1	-
X ₂₀	Pearl ⁴	25	0.5	2.8	0.8	4.7	1.0
X ₂₁	PI 109839	6	1.4	29.2	12.5	50.0	17.1
X ₂₂	PI 121067	28	2.0	9.3	3.1	25.0	6.4
X ₂₃	PI 138870	3	0.4	16.7	12.5	25.0	7.2
X ₂₄	PI 152125	1	0.2	25.0	25.0	25.0	-
X ₂₅	PI 161317	11	1.7	19.3	12.5	50.0	11.7
X ₂₆	PI 162858	3	0.5	20.8	12.5	25.0	7.2
X ₂₇	PI 203396	8	2.3	37.5	25.0	50.0	13.4
X ₂₉	PI 261976	2	0.8	50.0	50.0	50.0	0.0
X ₃₀	PI 268709	2	0.6	37.5	25.0	50.0	17.7
X ₃₁	PI 331334 ³	13	4.8	47.1	12.5	50.0	10.4
X ₃₂	PI 337396	8	1.0	15.6	6.3	25.0	8.2
X ₃₃	PI 341879	2	0.2	12.5	12.5	12.5	0.0
X ₃₄	PI 343381	1	0.4	50.0	50.0	50.0	-
X ₃₅	PI 355987	1	0.8	100.0	100.0	100.0	-
X ₃₆	PI 365553	6	2.3	50.0	25.0	100.0	27.4
X ₃₇	PI 475871	2	0.8	50.0	50.0	50.0	0.0
X ₄₀	Small White Spanish 3x-1 ⁴	24	1.0	5.5	1.6	9.4	2.1
X ₄₁	Small White Spanish 3x-2 ²	90	10.8	15.3	1.6	37.5	7.7
X ₄₂	Southeastern Runner	14	0.5	5.0	0.8	12.5	3.1
X ₄₃	Spanish 18-38 ¹	92	6.4	9.0	0.8	25.0	4.3
X ₄₄	Improved Spanish 2B	42	2.8	8.4	3.1	25.0	4.3
X ₄₆	Spantex	13	3.7	36.5	12.5	100.0	25.7
X ₄₇	T1861	4	0.3	10.9	6.3	12.5	3.1
X ₄₉	Unknown	4	1.6	50.0	50.0	50.0	0.0
X ₅₀	VA A89-5	3	0.2	10.4	6.3	12.5	3.6
X ₅₁	Valencia 803	3	1.2	50.0	50.0	50.0	0.0
X ₅₂	Virginia Bunch	1	0.4	50.0	50.0	50.0	-
X ₅₆	Virginia Jumbo Runner ⁴	24	0.3	1.4	0.4	2.3	0.5
X ₅₇	Virginia Runner ²	15	1.1	9.6	1.6	25.0	6.2
X ₅₉	White's Runner	22	1.7	9.9	0.8	31.3	8.3

^aAncestors with the same superscript number exhibited linear dependency in their genetic contributions to descendants.

ancestors appeared in the pedigrees of five or fewer lines: *A. monticola* Krapov. and Rigoni, Argentine, Chalimbana, Dixie Spanish, Makulu Red, NC Runner, PI 138870, PI 162858, PI 261976, PI 268709, PI 341879, PI 343381, PI 475871, T1861, VA A89-5, Valencia 803, and Virginia Bunch. These lines accounted for 11% of the ancestry of the overall sample. Four lines traced to at least one unknown ancestor.

Environments, i.e., combinations of years and locations, were a highly significant source of variation as previously found in other subsets of these data (Pattee *et al.*, 1993, 1994) (Table 2). Use of the covariates fruity attribute and linear and quadratic effects of roast color resulted in highly significant reductions in the error mean square, which agrees with previous reports (Pattee and Giesbrecht, 1994; Pattee *et al.*, 1994). Genotypes adjusted for all other model effects accounted for 11.4% of the total corrected sum of squares for roasted peanut attribute. This is close to earlier estimates of broad-sense heritability on a single-plot basis ($H = 0.11$ to 0.24) (Pattee and Giesbrecht, 1994).

When all 47 ancestors were included in a multiple regression analysis, there were eight linear dependencies so that only 39 ancestors could be included and still maintain estimability of ancestral effects. The contributions of Basse and Spanish 18-38 were completely confounded because they passed genes to descendants only

Table 2. Analysis of variance of roasted peanut flavor of 128 peanut cultivars and breeding lines.

Source	df	SS	R_G^2 ^a	
			Score	%
Total	694	637.58	—	0.92
Environment	29	97.24	—	3.35**
Fruity	1	46.08	—	46.08**
Roast color (linear)	1	11.70	—	11.70**
Roast color (quadratic)	1	10.97	—	10.97**
Genotype	127	72.42	—	0.57**
Ancestors	39	38.14	52.7	0.98**
Ancestors retained in model	13	33.14	45.7	2.55**
Atkins Runner	1	2.30	3.2	2.30**
Dixie Giant / SWS 3x-2	1	1.04	1.4	1.04*
Improved Spanish 2B	1	1.18	1.6	1.18*
Jenkins Jumbo	1	9.13	12.6	9.13**
Makulu Red	1	3.48	4.8	3.48**
PI 109839	1	1.20	1.7	1.20*
PI 161317	1	0.61	0.8	0.61
PI 203396	1	2.04	2.8	2.04**
PI 261976	1	4.30	5.9	4.30**
PI 365553	1	4.77	6.6	4.77**
VA A89-5	1	0.63	0.9	0.63
Valencia 803	1	0.88	1.2	0.88*
Virginia Bunch	1	3.82	5.3	3.82**
Residual ancestral effect	26	5.00	6.9	0.19
Residual genotypic effect	88	34.28	47.3	0.39**
Error	535	107.78	—	0.20

*, **Denote significance at the 5% and 1% levels of probability, respectively.

^aDenotes the coefficient of multiple determination using the partial sum of squares for genotypes as denominator.

through sibling lines derived from Univ. of Georgia cross GA 207. Similarly, Krinkle Leaf and PI 331334 contributed only through a single cross made at the Univ. of Georgia (Branch, 1991). The contribution of Small White Spanish 3x-2 was confounded with that of Dixie Giant in Univ. of Florida cross F231. NC Bunch and PI 121067 contributed only through cross "C" made by W.C. Gregory at North Carolina State Univ. The effects of Pearl, Small White Spanish 3x-1, and Virginia Jumbo Runner (Jumbo F14-3) were confounded with linear combinations of McSpan Spanish and NC Runner in the ancestry of Univ. of Florida cross F406, source of the cultivar Early Bunch. Contributions from Southeastern Runner and Virginia Runner were also confounded with linear combinations of Dixie Giant, McSpan Spanish, NC Runner, and Small White Spanish 3x-2.

The remaining 39 ancestors accounted for 53% of the sum of squares due to genotypic effects or 6% of the total phenotypic variation. Because the effects of ancestors over several generations must be additive in nature, this proportion (6%) may be used as a crude estimate of narrow-sense heritability. The utility of this estimate has several limitations. First, the reference population to which it should be applied is not obvious. There is no single panmictic U.S. breeding population in the true sense. The U.S. population has been divided into subpopulations developed for the various production regions. Second, the cultivars and, to a lesser extent, the breeding lines submitted for evaluation of flavor represent a population in which some selection for acceptable flavor has occurred. This may have served to reduce the genotypic variation for roasted peanut attribute. Nevertheless, until estimates of narrow-sense heritability are obtained for specific populations designed for the purpose of estimation, this is the only estimate extant. The remaining 47.3% of the genotype sum of squares represented a highly significant amount of the variation, indicating that nonadditive genetic effects are important in the determination of roasted peanut flavor. There was no obvious method to parameterize the regression model to account for this variation and the 88 degrees of freedom associated with it.

Identification of ancestors with beneficial or deleterious effects on roasted peanut flavor required that the regression model be reduced, eliminating ancestors with nonsignificant effects that might obscure those of important ancestors. The C_p value for the best model of a given size was close to the number of parameters for two models at $p = 133$ (12 ancestors, $C_p = 133.8$ and $C_p = 133.9$) and less than the number of parameters for $p = 134$ (13 ancestors, $C_p = 132.8$). The best model at $p = 134$ included all the ancestors in the two best models at $p = 133$ and was also the best model where $C_p < p$, so it was accepted as the smallest model to adequately fit the data. Ancestors included in this model were, in order of inclusion based on forward selection using the MAXR option: Jenkins Jumbo, Dixie Giant / Small White Spanish 3x-2, PI 365553, Virginia Bunch, PI 203396, PI 109839, Atkins Runner, VA A89-5, PI 261976, Makulu Red, Improved Spanish 2B, Valencia 803, and PI 161317. These 13 ancestors accounted for nearly half (46%) of the variation

attributable to genotypes or 87% of the variation attributable to all ancestors. Jenkins Jumbo alone accounted for over 12% of the variation among genotypes after accounting for all other important ancestors. After fitting the model with 13 ancestors, the residual variation due to ancestors was only 6.9% of the genotypic variation and was not significant.

The estimated regression coefficients (b 's, Table 3) represent the deviation from the population mean roasted peanut flavor one would expect to measure on the ancestor itself. Half of that effect would be transmitted to the progeny of a single cross, one quarter to grandprogeny, and one eighth to great-grandprogeny. Only three of these ancestors (Dixie Giant / Small White Spanish 3x-2, Valencia 803, and Virginia Bunch) had significant positive effects on the roasted peanut flavor of their descendants. The remaining ancestors all had negative effects. Based on the significance of the nonadditive portion of the genotype sum of squares and the finding that most measurable ancestral effects on flavor were negative, it appears that genetic control of roasted flavor is complex, involving epistatic interactions so that good flavor can be decreased by the presence of deleterious genes.

In building the ancestral regression model, Jenkins Jumbo was the first ancestor included, indicating that its ancestral contribution had the strongest simple correlation with roasted flavor in its descendants. It also had the strongest relationship when the contributions of other important ancestors were taken into account. While other ancestors had greater negative effects than Jenkins Jumbo ($b_{11} = -1.25$), it was the most ubiquitous deleterious ancestor in the pedigrees of lines assayed for flavor. Jenkins Jumbo was initially used in the Univ. of Florida breeding program as a source of large pod and seed size. While it made no contribution to the ancestry of the 10 spanish-type lines tested, it is common in the pedigrees of virginia- and runner-type lines, contributing to 52 of

62 virginia descendants and 22 of 55 runner descendants primarily through crosses F359 and F393. F359 was a forerunner of the popular virginia-type cultivar Florigiant. Two cultivars, NC-Fla 14 and NC 17, were selected from F393 which was also a parent of NC 7. Jenkins Jumbo is also an ancestor of the cultivar Early Bunch through Florida cross F385. Through Florigiant and NC 7, Jenkins Jumbo is an ancestor of most breeding lines in the North Carolina peanut breeding program. Based on the estimate of Jenkins Jumbo's effect, its progeny from single crosses may be expected to exhibit a reduction of 0.62 units in roasted peanut flavor, its grandprogeny 0.31 units, and its great-grandprogeny 0.16 units. A change of 0.5 units is considered to be significant in terms of consumer preference (Pattee and Giesbrecht, 1990). Improved Spanish 2B ($b_{44} = -1.05$) was the only other common ancestor to exert a significant effect on roasted peanut flavor. This ancestor was used in the North Carolina breeding program and gave rise to NC 6 through its progenitor, GP-NC 343, and to NC 5 which in turn gave rise to NC 7 and the recently released cultivar VA-C 92R. The only ancestor to be common in the pedigrees of the lines tested and having a positive influence on roasted flavor ($b_7 = 0.44$) was F231, the Dixie Giant / Small White Spanish 3x-2 cross that was a progenitor of cultivars Early Runner, Florispan Runner, Florunner, and Florigiant.

The rest of the ancestors found to significantly influence flavor were present in the pedigrees of relatively few (1 to 11) of the lines tested. These parents have been used by peanut breeders for various purposes. PI 109839 is known to carry resistance to early leaf spot (*Cercospora arachidicola* Hori) (Hammons, 1980). It is fortuitous that it also transmits better roasted flavor to its progeny. Similarly, PI 203396 carries resistance to late leaf spot [*Cercosporidium personatum* (Berk. & Curt.) Deighton] and was a parent of the moderately resistant cultivar Southern Runner (Gorbet *et al.*, 1987), but in this case the source of resistance reduces the roast flavor of its progeny. These results confirm that breeders should exercise caution when incorporating germplasm into their breeding populations for improvement of specific traits: the effect of such parents on flavor may be deleterious. Flavor of disease- or pest-resistant selections should be evaluated as soon as practical in the breeding process.

It has been documented that the average roasted peanut attribute score for virginia market types is less than that for runners although there is substantial overlap in the distributions of flavor scores for the two classes (H.E. Pattee, F.G. Giesbrecht, and T.G. Isleib, unpubl. data). The basis for this difference, whether a negative physiological association between large seed size and less intense flavor, pleiotropy or negative genetic linkage of genes controlling seed size and flavor, or some other cause, has not been determined. The results of this study imply that there were significant differences in flavor among the progenitors of the U.S. peanut gene pool, and that those differences have persisted through the four to six cycles of recombination that have occurred since the inception of peanut breeding programs. Although there

Table 3. Ancestral contributions of 13 progenitors to roasted peanut intensity scores of 128 peanut cultivars and breeding lines.

Ancestor	Estimate (b)	Standard error	t	Order of entry in model
----- Score -----				
Atkins Runner	-1.16	0.34	-3.38**	8
Dixie Giant / SWS 3x-2	+0.44	0.19	2.27*	2
Improved Spanish 2B	-1.05	0.44	-2.42*	11
Jenkins Jumbo	-1.25	0.19	-6.73**	1
Makulu Red	-4.17	1.00	-4.16**	6
PI 109839	+0.74	0.30	2.44*	9
PI 161317	-0.48	0.28	-1.74	13
PI 203396	-0.64	0.20	-3.18**	7
PI 261976	-1.33	0.29	-4.62**	5
PI 365553	-1.74	0.36	-4.86**	3
VA A89-5	+3.33	1.88	1.77	10
Valencia 803	+0.79	0.38	2.09*	12
Virginia Bunch	-3.31	0.76	-4.35**	4

*,**Denote significance at the 5% and 1% levels of probability, respectively.

is common ancestry in the pedigrees of virginia and runner cultivars and lines, there are also distinctions between the two (Table 4), particularly when comparing

lines developed at different institutions. For example, some of the difference between market classes might be ascribable to differences in the ancestors used in North

Table 4. Frequency of appearance and average genetic contribution of 47 ancestral lines to 127 cultivars and breeding lines of runner, virginia and spanish market-types.

Ancestor	Overall freq.	Runner (n=55 ^a)			Virginia (n=62)			Spanish (n=10)		
		Mean ^b	Mean if present ^c	Freq.	Mean	Mean if present	Freq.	Mean	Mean if present	Freq.
		----- %	----- %		----- %	----- %		----- %	----- %	
<i>Arachis monticola</i>	3	0.2	12.5	1	0.0	—	0	3.8	18.8	2
Argentine	5	4.5	62.5	4	0.1	6.3	1	0.0	—	0
Atkin's Runner	7	0.0	—	0	3.2	28.6	7	0.0	—	0
Basse	92	5.1	7.4	38	8.6	10.1	53	0.6	6.3	1
Chalimbana	1	0.0	—	0	0.8	50.0	1	0.0	—	0
Chico	8	1.8	100.0	1	4.0	50.0	5	10.0	50.0	2
Dixie Giant	91	14.3	20.7	38	12.6	15.0	52	1.9	18.8	1
Dixie Spanish	1	0.0	—	0	0.2	12.5	1	0.0	—	0
Holland Station Jumbo	19	1.9	10.3	10	1.6	10.8	9	0.0	—	0
Jenkins Jumbo	74	5.5	13.7	22	14.2	16.9	52	0.0	—	0
Krinkle Leaf	13	11.1	47.1	13	0.0	—	0	0.0	—	0
Makulu Red	1	0.5	25.0	1	0.0	—	0	0.0	—	0
McSpan Spanish	24	0.3	1.5	12	0.3	1.3	12	0.0	—	0
NC 4	35	0.0	—	0	4.1	7.3	35	0.0	—	0
NC Bunch	28	0.0	—	0	4.2	9.3	28	0.0	—	0
NC Runner	1	0.0	—	0	0.1	3.1	1	0.0	—	0
Pearl	25	0.6	2.9	12	0.6	2.6	13	0.0	—	0
PI 109839	6	3.2	29.2	6	0.0	—	0	0.0	—	0
PI 121067	28	0.0	—	0	4.2	9.3	28	0.0	—	0
PI 138870	3	0.0	—	0	0.8	16.7	3	0.0	—	0
PI 152125	1	0.0	—	0	0.0	—	0	2.5	25.0	1
PI 161317	11	0.2	12.5	1	0.4	12.5	2	17.5	21.9	8
PI 162858	3	0.0	—	0	1.0	20.8	3	0.0	—	0
PI 203396	8	5.5	37.5	8	0.0	—	0	0.0	—	0
PI 261976	2	0.9	50.0	1	0.8	50.0	1	0.0	—	0
PI 268709	2	0.9	50.0	1	0.4	25.0	1	0.0	—	0
PI 331334	13	11.1	47.1	13	0.0	—	0	0.0	—	0
PI 337396	8	0.0	—	0	2.0	15.6	8	0.0	—	0
PI 341879	2	0.5	12.5	2	0.0	—	0	0.0	—	0
PI 343381	1	0.0	—	0	0.8	50.0	1	0.0	—	0
PI 355987	1	0.0	—	0	0.0	—	0	0.0	—	0
PI 365553	6	5.5	50.0	6	0.0	—	0	0.0	—	0
PI 475871	2	1.8	50.0	2	0.0	—	0	0.0	—	0
Small White Spanish 3x-1	24	1.3	5.9	12	1.0	5.2	12	0.0	—	0
Small White Spanish 3x-2	90	12.6	18.2	38	10.8	13.2	51	1.9	18.8	1
Southeastern Runner	14	0.5	6.3	4	0.7	4.5	10	0.0	—	0
Spanish 18-38	92	5.1	7.4	38	8.6	10.1	53	0.6	6.3	1
Improved Spanish 2B	42	1.1	15.6	4	4.1	7.3	35	3.8	12.5	3
Spantex	13	0.5	25.0	1	0.4	12.5	2	42.5	42.5	10
T1861	4	0.5	12.5	2	0.3	9.4	2	0.0	—	0
Unknown	4	1.8	50.0	2	1.6	50.0	2	0.0	—	0
VA A89-5	3	0.0	—	0	0.5	10.4	3	0.0	—	0
Valencia 803	3	0.0	—	0	0.0	—	0	15.0	50.0	3
Virginia Bunch	1	0.0	—	0	0.8	50.0	1	0.0	—	0
Virginia Jumbo Runner	24	0.3	1.5	12	0.3	1.3	12	0.0	—	0
Virginia Runner	15	0.9	12.5	4	1.5	8.5	11	0.0	—	0
White's Runner	22	0.0	—	0	3.5	9.9	22	0.0	—	0

^a"n=" denotes the number of cultivars and lines in the market class.

^b"Mean" denotes the mean contribution of the progenitor to all lines in the market class.

^c"Mean if present" denotes the mean contribution of the progenitor to descendants in the market class.

Carolina and Virginia, e.g., Improved Spanish 2B and Atkins Runner, vs. those used in Florida and Georgia even through joint research efforts between institutions and the release of successful cultivars have resulted in intermingling of the states' breeding populations. PI 203396 has been used only in the Florida and Georgia programs. PI 365553 (TxAg-3), a line resistant to soil-borne fungal diseases (O.D. Smith, pers. commun.) appears only in the pedigrees of runner-type lines from Texas. Likewise, the ancestry of the spanish market-type is broadly distinct from the virginia and runner-types. Spantex and PI 161317 appear much more frequently and with much larger average contributions in the ancestry of spanish-type lines than in runner- and virginia-type lines. Valencia 803 appears only in the pedigrees of spanish-type lines.

In addition to differences in which ancestors form the genetic base for different programs and market-types, there are differences in the magnitudes of contribution from common ancestors. F231 (Dixie Giant / Small White Spanish 3x-2) appears in the pedigrees of 38 of the 55 runner types evaluated in this study and made an average contribution of 21% to the ancestry of those 38 lines. In contrast, it contributed only 13% of the ancestry in 52 of 62 virginia lines for which it was a progenitor. Likewise, Jenkins Jumbo made a greater average contribution to virginia lines than it did to runner lines (17% of ancestry in 52 of 62 lines vs. 14% in 22 of 55 lines). Breeders of virginia-type cultivars may wish to reduce the contribution of Jenkins Jumbo to their breeding lines by consciously avoiding the use of parents descended from Jenkins Jumbo or other ancestors with negative effects on flavor. They may also improve peanut flavor by increasing the contributions to breeding populations from lines with no or low coancestry with deleterious ancestors. This could be achieved by backcrossing or by convergent crosses. Similar techniques could be used to increase the contribution of F231 and other ancestors

with beneficial effects on flavor. It should be pointed out that there were 26 progenitors, i.e., those not included in the 13-progenitor regression model, whose effects on flavor were essentially neutral. Use of these lines or their descendants as parents in breeding programs should have no predictable effect on flavor.

Literature Cited

1. Branch, W.D. 1991. Registration of 'Georgia Runner' peanut. *Crop Sci.* 31:485.
2. Falconer, D.F. 1981. *Introduction to Quantitative Genetics*, 2nd Ed. Longman, New York.
3. Gorbet, D.W., A.J. Norden, F.M. Shokes, and D.A. Knauff. 1987. Registration of 'Southern Runner' peanut. *Crop Sci.* 27:817.
4. Hammons, R.O. 1980. Registration of *Cercospora arachidicola*-resistant peanut germplasm. *Crop Sci.* 20:292.
5. Isleib, T.G., and J.C. Wynne. 1992. Use of plant introductions in peanut improvement, pp. 75-116. In H.L. Shands and L.E. Weisner (eds.) *Use of Plant Introductions in Plant Improvement*, Part 2. CSSA Spec. Publ. No. 20. *Crop Sci. Soc. Amer.*, Madison, WI.
6. Knauff, D.A., and D.W. Gorbet. 1989. Genetic diversity among peanut cultivars. *Crop Sci.* 29:1417-1422.
7. Neter, J., and W. Wasserman. 1974. *Applied Linear Statistical Models*. Richard D. Irwin, Inc. Homewood, IL.
8. Pattee, H.E., and F.G. Giesbrecht. 1990. Roasted peanut flavor variation across germplasm sources. *Peanut Sci.* 17:109-112.
9. Pattee, H.E., and F.G. Giesbrecht. 1994. Adjusting roasted peanut attribute scores fruity attribute and non-optimum CIELAB L* values. *J. Sens. Studies* 9:353-363.
10. Pattee, H.E., F.G. Giesbrecht, and T.G. Isleib. 1994. Genotype-by-environment interaction in roasted peanut attribute. *Peanut Sci.* 22: 94-99.
11. Pattee, H.E., F.G. Giesbrecht, and R.W. Mazingo. 1993. A note on broad-sense heritability of selected sensory descriptors in virginia-type *Arachis hypogaea* L. *Peanut Sci.* 20:24-26.
12. Pattee, H.E., F.G. Giesbrecht, and C.T. Young. 1991. Comparison of peanut butter color determination by CIELAB L*a*b* and Hunter color-difference methods and the relationship of roasted peanut color to roasted peanut flavor response. *J. Agric. Food Chem.* 39:519-523.
13. SAS Institute, Inc. 1990. *SAS/STAT User's Guide*, Vers. 6, Fourth Ed. SAS Institute, Inc. Cary, NC.

Accepted 13 February 1995