

Quantitative Genetic Analysis of Fruit Quality in Pear

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Abstract. Narrow-sense heritability estimates were computed for five fruit quality characteristics and their weighted total index. Grit content and skin russeting were moderately heritable traits, while flesh texture, flavor, appearance, and the weighted total score were of relatively low heritability. Within sub-populations of crosses, defined by the species ancestry of the parents, the relative magnitudes of heritabilities for each trait varied, but were in general agreement with those for the entire population. The general combining ability variances were 4.5 to 12.0 times those for specific combining ability, although both were statistically significant for all traits and the weighted quality index. The species ancestry of a parent had no effect on its general combining ability rank. While selection of individual seedlings on the basis of their own phenotype will result in genetic improvement for grit and russet, selection based on a combination of full-sib family means and individual phenotypes is recommended for flavor, texture, appearance, and overall fruit quality.

Various component traits affect overall fruit quality of pears, including flavor, grit (stone cell) content, flesh texture, skin russet, and appearance. The inheritance of the major economically important fruit quality characteristics has been reviewed by Layne and Quamme (1975) and Bell (1978, 1982). Much of the earlier work focused on detection of major genes, particularly within interspecific crosses, and has traditionally used analysis of segregation patterns of more or less distinct classes.

These characteristics are inherited in a complex polygenic manner, with progenies characterized by continuous distributions. Thompson et al. (1974) concluded that, in crosses involving species that contain grit cells [*P. communis* L., *P. ussuriensis* Maxim., *P. pyrifolia* (Burro.) Nakai, and *P. calleryana* Decne.], grit content was inherited quantitatively and was determined by a minimum of four loci acting with additive, rather than dominant, effects. Within *P. communis*, russet appears to be quantitatively inherited (Crane and Lewis, 1949; Zielinski et al., 1965). Depending on the parents, Zielinski et al. (1965) obtained evidence for both polygenic and monogenic control of juiciness, but concluded that flavor (i.e., a subjective rating of sugar/acid balance) was determined by several recessive genes. This conclusion is supported by evidence reported by Bell et al. (1981). The only study of objective measures of fruit flavor components indicated that soluble solids and juice pH were independently and additively inherited (Visser et al., 1968). Lantz (1929) characterized the inheritance of fruit texture and flavor in *P. communis* × *P. ussuriensis* hybrid progenies as being quantitative, with some apparent "dominance" of coarse texture and poor flavor.

Heritability is a measure of the proportion of variability in phenotype due to genetic factors. Narrow-sense heritability is

an estimate of the proportion due to average, or additive, genetic effects. It is a measure of the degree to which parental phenotype predicts the phenotypic mean of their progeny. An allied technique, combining ability analysis, partitions phenotypic variance among progeny means into components due to the additive contributions of individual parents (general combining ability), and the variance due to interactions among parents (specific combining ability), and can estimate the relative breeding value of the parents. The objectives of this study were to obtain estimates of narrow-sense heritability and of general and specific combining ability for fruit quality traits in a pear breeding population. The results could then be used in assessing the efficacy of alternate selection strategies and in selecting parents for future crosses.

Material and Methods

The population. Our study was based on the breeding records of the USDA pear breeding program at Beltsville, Md., and used data on progenies planted from 1962 through 1966. The 99 cultivars and selections used as parents were selected primarily on the basis of fire blight resistance or desirable fruit quality traits, and, therefore, constitute a fixed rather than a random sample from a population. The parents consisted of 42 genotypes of *P. communis*, 12 *P. communis* × *P. pyrifolia* hybrids, nine hybrids for which one parent was *P. communis*, and the other was of unknown species, one *P. communis* × *P. ussuriensis* hybrid, one *P. calleryana* cultivar, one of *P. communis* × (*P. ussuriensis* × *P. pyrifolia*) parentage, and two of unknown pedigree. The crosses were made solely for the purpose of genetic improvement without regard to a specific mating design. The usual assumption of random mating was not strictly met, and parents were used in varying numbers of crosses. A total of 271 biparental matings were made, of which 137 were represented by reciprocal crosses. The progeny planted in any one year constituted a unique set, with only 20 crosses, or 7.8%, being replicated over years. Number of evaluated progeny per cross varied from one to 92 seedlings, with 78% of the crosses with 10 or more seedlings. A total of 2754 seedlings were evaluated for fruit quality.

Fruit quality evaluations. Data on seedlings were collected for 1 to 6 years from 1965 through 1976, while parents were evaluated for 1 to 8 years from 1961 through 1968, with an average of 3.9 years. Fruit samples of seedlings and 74 of their parents were harvested, stored, and evaluated subjectively as

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described previously (Bell, 1978; Bell et al., 1976; Blake and van der Zwet, 1979). The number of harvests and time in storage varied, with no uniform plan used in all years. Fruit quality is affected by harvest date, including both premature and delayed harvest, and duration of storage. (Batjer, 1967). Samples were stored for 7 to 135 days, within the recommended range for most major cultivars. The mean of all samples harvested on the same date was computed. For seedlings, only 3% of the harvest dates had multiple storage samples. Harvests were conducted for up to 4 weeks to estimate proper harvest date, and, therefore, some individual samples were probably outside of the period during which valid evaluation of fruit quality could be expected. Analysis of parental data had indicated that variation due to harvest date was significant (Bell, 1978). To eliminate possible bias due to improper harvest date, the highest harvest date mean was selected as being representative of the unbiased genetic potential of a genotype in each year. Analysis of variance had also determined that there were significant differences among year means for parents. Because not all parents were evaluated in a concurrent set of years, yearly parental scores were adjusted for fixed-year effects computed from a set of seven parents that had been evaluated from 1961 through 1968. Parental means were computed using the adjusted yearly scores. Parents not evaluated during these 8 years and their offspring were not included in the data set used for estimation of heritability by parent-offspring regression. No adjustment was made in seedling data, since few seedlings were evaluated for >1 year, and no set of parents were evaluated over the entire period of seedling evaluation.

Each observation represents a mean of two or three trained evaluators' scores for a sample of six fruit. Five fruit quality traits were scored using a subjective scale of 1 (worst) to 9 (best). For the purposes of this analysis, it was assumed that each point on the phenotypic scale represents equal increments on an underlying scale of additive genetic effects. A weighted total score, used as a selection index, was computed. The weights were chosen on the basis of the presumed relative importance of each trait to consumer appeal, and was therefore similar to a base index (Williams, 1962). The traits and their respective weights are as follows: flavor (4×), grit (3×), texture (2×), russet (1×), and appearance (1×).

Heritability estimation. Because the number of progeny per family differed, parental effects would be disproportionately represented in a regression of individual seedling values on the corresponding mean of the parents. To reduce this source of bias in the estimation of narrow-sense heritability, a regression of weighted family means was employed (Reeve, 1955). The appropriate weights were based on progeny count and the heritability computed by regression of unweighed family means on mid-parental value for each trait.

In addition to the heritabilities estimated for the entire population, subpopulations classified by the species pedigree of the parents, hereafter referred to as species crosses, were analyzed by the weighted regression method. In each of these methods, the unstandardized regression coefficient estimates narrow-sense heritability of individual scores ($b = h^2$). Because all parents had not been evaluated in the years used to compute yearly adjustment factors, heritabilities were computed from a restricted subpopulation of crosses and parents.

Estimation of heritability by parent-offspring regression requires the assumption that the parents are derived from a random mating population with no linkage disequilibrium, and that genotypic and environmental effects are additive and uncorrelated.

The parents used in this breeding population are a fixed set, and inferences made from the analyses are strictly applicable only to that set. However, they do represent the base for the breeding program, and it is the population of interest to the breeder. Selection of the parents does not affect the estimation of heritability of offspring on parent, since the covariance of offspring and parents is reduced to the same extent as the variance of the parents (Falconer, 1981). Random mating of the parents guarantees that no parent disproportionately contributes to the offspring population. Some bias of unknown magnitude and direction as a result of violating this assumption is acknowledged. Some genotype-environment correlation is also probable as a result of nonrandomization of seedlings and parents within the orchard and the lack of fruit evaluation of all genotypes within the same set of years.

Combining ability. For computing the analysis of variance for combining ability, and for computing general combining ability (GCA) constants for each parent, the least-squares fitting of constants method, as outlined by Gilbert (1967), was employed. The analysis partitioned effects due to GCA and specific combining ability (SCA). Residual error is due to phenotypic variance among seedlings within crosses. A random model was assumed, and coefficients of variance components were calculated according to procedures outlined by England (1974) for incomplete and unbalanced diallels. Because the parents were highly heterozygous (Bell et al., 1981), the variance is due to genetic differences among full-sib error variance, and is biased by genotype-environment correlation associated with the manner of data collection. The program also pools replicates of crosses as well as reciprocals within the residual mean square. General combining ability constants for each parent, g_{ij} , are defined as the additive combining ability effect of the i^{th} or j^{th} parent as a deviation from the seedling population mean.

Few crosses from which some g_{ij} were calculated were recognized as contributing to large standard errors of some estimates. For this reason, individual g_{ij} were tested for significance of deviation from the parental mean GCA ($H_0: g_i = 0$) by means of a one-tailed t test in which $t = g_{ij}/SE$ of g_{ij} for $c - 1$ degrees of freedom, where c is the number of crosses involving the parent.

The computational method required that each parent be represented in a minimum of two crosses and that all parents be interconnected through matings to common parents. These restrictions have resulted in another subpopulation of crosses and parents that is somewhat different from the original population and from that used to compute heritabilities by regression on mid-parental values.

The estimation of combining ability requires the same assumptions discussed above for heritability. An additional assumption is that the parents be unrelated, and, therefore the progenies will be non-inbred. Failure to meet this assumption will bias the estimates of genetic variance upwards. The parents should also be non-inbred or inbred to the same degree. Inbreeding of the progenies can bias the estimates of additive genetic variance upward. In the present study, only one parent was inbred (US-Michigan 437; $F = 0.25$), but was used in only three crosses. Nearly half of the progeny were inbred to some degree, but the average value, 0.08, was of little concern (Bell et al., 1981).

Results and Discussion

Parental mean score for flavor ranged from 2.7 to 7.5, with a mean of 5.0; mean grit score ranged from 1.7 to 8.5, with

Table 1. Heritability estimates for fruit quality traits, computed by unweighed and weighted regression, for all progenies and by species cross.

Regression method and population	n	Flavor			Grit			Texture			Russet			Appearance			Weighted total score		
		h ²	SE _{h²}	P ^y	h ²	SE _{h²}	P	h ²	SE _{h²}	P	h ²	SE _{h²}	P	h ²	SE _{h²}	P	h ²	SE _{h²}	P
Unweighed individual scores																			
All progenies	2179	0.25	0.03	0.01	0.57	0.03	0.01	0.30	0.03	0.01	0.51	0.02	0.01	0.17	0.03	0.01	0.17	0.02	0.01
Weighted family means																			
All progenies	217 ^x	0.21	0.02	0.01	0.54	0.03	0.01	0.30	0.02	0.01	0.52	0.02	0.01	0.18	0.02	0.01	0.16	0.01	0.01
Species crosses																			
<i>communis</i> × <i>communis</i>	94 ^x	0.06	0.04	0.14	0.48	0.06	0.01	0.14	0.04	0.01	0.51	0.03	0.01	0.18	0.04	0.01	0.07	0.02	0.01
<i>communis</i> × <i>communis</i> - <i>pyrifolia</i>	65	0.23	0.04	0.01	0.54	0.04	0.01	0.31	0.04	0.01	0.57	0.04	0.01	0.21	0.03	0.01	0.03	0.02	0.17
<i>communis</i> × unknown	31 ^x	0.33	0.34	0.01	0.73	0.05	0.01	0.39	0.06	0.01	0.39	0.05	0.01	0.07	0.04	0.07	0.41	0.03	0.01
<i>communis</i> - <i>pyrifolia</i> × <i>communis</i> - <i>pyrifolia</i>	12	0.08	0.06	0.19	0.55	0.08	0.01	0.16	0.05	0.01	0.94	0.10	0.01	0.27	0.08	0.01	0.23	0.05	0.01
<i>communis</i> - <i>pyrifolia</i> × unknown	6	0.23	0.06	0.01	0.93	0.24	0.01	0.95	0.12	0.01	0.52	0.11	0.01	0.38	0.07	0.01	0.19	0.05	0.01
unknown × unknown	7	0.54	0.05	0.01	0.43	0.06	0.01	0.35	0.07	0.01	0.67	0.10	0.01	0.33	0.02	0.01	0.35	0.04	0.01

^zSE_{h²} is the standard error of the estimate of heritability.

^yP is the probability of type I error for the hypothesis H₀:h² = 0.

^xNumber of weighted family means for grit, russet, and appearance were 222, 97, and 33, respectively, for all progenies, *communis* × *communis* crosses, and *communis* × unknown crosses.

Table 2. Summary of analyses of variance components (σ²) of general (GCA) and specific (SCA) combining ability for fruit quality traits.

Source	Grit		Russet		Texture		Flavor		Appearance		Weighted total score	
	df	σ ²	df	σ ²	df	σ ²	df	σ ²	df	σ ²	df	σ ²
GCA	67	0.63**	67	0.59**	67	0.34**	67	0.18**	67	0.21**	67	28.33**
SCA	218	0.07*	218	0.07**	211	0.05*	207	0.04**	218	0.04**	207	2.36**
Residual	2259	1.47	2261	1.41	2179	0.72	2174	0.63	2261	0.84	2174	50.25

a mean of 6.0; mean texture score ranged from 2.4 to 7.9, with a mean of 5.6; mean russet score ranged from 1.0 to 8.2, with a mean of 5.5; mean appearance ranged from 1.6 to 7.6, with a mean of 5.2; and total weighted score ranged from 34.7 to 79.0, with a mean of 59.9. Seedling flavor scores ranged from 1 to 7, with a mean of 3.9; grit ranged from 1 to 9, with a mean of 5.6; texture ranged from 2 to 8, with a mean of 4.9; russet. ranged from 1 to 9, with a mean of 4.9; appearance ranged from 1 to 8, with a mean of 3.9; and weighted total score ranged from 10 to 80, with a mean of 50.7. The distribution of seedling scores for all traits and the weighted total score are continuous, and without marked skewness, which would indicate dominance of a few genes (Bell, 1978).

Heritability. All unweighed regressions were highly significant (Table 1). The heritabilities (h²) of individual seedling values for grit (0.57) and russet (0.51) were moderately high, texture (0.30) and flavor (0.25) were intermediate, while appearance (0.18) and weighted total score (0.17) were relatively low. Heritability of weighted full-sib family means (h_f²) agreed very closely with the heritability of individual seedling values (Table 1).

The heritability estimates for flavor scores were, in general, low (0.21 for the entire population and ranging from 0.06 to 0.54 for the various species crosses). Heritabilities differed significantly from zero in only four of the six species crosses. These results are not surprising for a complex trait that depends on various underlying components, environmental influences, and their interactions. Nongenetic sources of variability, such as yearly climatic differences, harvest dates, and length of storage, are known to influence flavor scores (Bell, 1978). In a previous study, percent soluble solids content and juice pH, the ratio of which contributes to overall flavor, were found to be additively inherited (Visser et al., 1968). The major genetic

determinants of flavor in our population were also additive in nature.

Grit content was moderately heritable (0.54). Within species cross subpopulations, heritabilities varied between 0.48 for crosses within *P. communis* to 0.93 for crosses between parents of *P. communis*-*P. pyrifolia* and those of unknown parentage. The latter subpopulation is based on only six progenies and is therefore of little predictive value for other parents and crosses. No evidence of marked dominance was found, as was previously reported (Westwood and Bjornstad, 1971; Golisz et al., 1971; Zielinski et al., 1965). The results are in agreement with those of Thompson et al. (1974), who postulated genetic control by a minimum of four genes, each acting in a predominantly additive fashion. The results do not rule out the possibility of a major gene allowing the development of grit (Layne and Quamme, 1975; Zielinski et al., 1971), but, rather, confirm the presence of additional additive genetic factors, resulting in continuous variation within and among seedling progenies. Grit content is known to be relatively stable over a broad range of environmental conditions (Crist and Batjer, 1931).

The estimated heritability for texture was 0.30 for the entire population. For the species subpopulations, all estimates were of about the same magnitude, with the exception of the *P. communis*-*P. pyrifolia* × unknown crosses, which had an unusually high value (0.95). The small number of crosses in this case and the resultant sampling variation probably accounts for some of the marked deviation from the other estimates. Texture is known to be affected considerably by environmental factors, and, thus, variance due to nongenetic factors is likely to be large. Environmental effects associated with year, harvest date, and ripening process can significantly influence texture scores (Bell, 1978; Layne and Quamme, 1975). Genetic progress, when parents are chosen solely on the basis of their own phenotypes, will be slower than for grit.

Table 3. Species, phenotypic scores (PS), and general combining ability constants (GCA) for 68 parents.

Parent	Species	Flavor			Grit			Texture			Russet			Appearance			Weighted total score		
		PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE
US 1284	C	---	1.0	0.6	4.5	-0.2	0.7	---	0.2	0.6	4.2	0.1	0.7	3.5	1.5	0.5	---	7.7	5.1
US-Mich 572 (4 ×)	C	3.4	0.2	0.4	3.3	1.3	0.6	3.7	0.8	0.4	5.9	0.2	0.6	5.9	0.9	0.5	42.6	7.1	3.5
NJ 5008710504	CP	4.7	0.2*	0.1	6.2	1.1***	0.2	5.9	0.5***	0.1	7.2	1.2***	0.2	7.6	0.8**	0.2	64.4	6.9***	1.2
US 446	C	5.7	0.3**	0.1	6.7	0.6***	0.1	6.2	0.7***	0.1	7.4	0.9***	0.1	7.6	0.7***	0.1	70.2	5.6***	0.8
US 250	C	4.2	0.7	0.2	5.4	0.3	0.3	4.5	0.2	0.2	5.8	1.0	0.3	3.8	0.3	0.2	51.6	5.2	1.9
US 56112-146	CX	6.4	0.0	0.1	7.7	1.2***	0.1	6.7	0.4**	0.1	6.5	0.4***	0.1	5.7	-0.0	0.1	74.2	4.9***	0.6
US 725	C	4.1	0.1	0.2	7.4	1.4***	0.2	6.0	0.5*	0.2	7.0	-0.3	0.2	6.8	-0.2	0.2	64.5	4.8*	1.4
US 56121-008	CX	6.5	0.7*	0.1	8.4	0.3	0.2	7.7	0.6	0.1	4.3	-0.3	0.2	5.2	0.1	0.2	76.2	4.4	1.2
US 278	C	5.3	0.1	0.1	8.0	0.8***	0.1	5.7	0.4***	0.1	5.5	0.6***	0.1	6.6	0.2	0.1	68.6	4.4***	0.8
Ananas de Courtrais	C	---	0.1	0.1	---	0.8**	0.2	---	0.2	0.1	---	0.8**	0.2	---	0.2	0.1	---	3.9	1.0
Charles Escaig	CX	---	0.1	0.2	---	0.6	0.3	---	0.3	0.2	---	0.6	0.3	---	0.7	0.2	---	3.9***	1.7
US 56112-119	CX	6.2	0.1	0.1	8.5	1.0***	0.1	6.9	0.1	0.1	7.0	0.2	0.1	5.6	0.1	0.1	76.6	3.9**	0.7
US 386	C	5.1	0.1	0.1	7.5	0.8***	0.2	5.4	0.4**	0.1	6.9	0.1	0.1	6.2	0.1	0.1	66.1	3.9***	0.8
Maxine	C	4.2	0.3	0.3	6.6	0.0	0.4	5.0	0.2	0.3	7.6	0.6	0.4	6.2	0.3	0.3	60.3	3.8	2.5
US 643	CP	6.1	0.2*	0.1	8.4	0.8***	0.1	7.6	0.4***	0.1	5.2	-0.3	0.2	4.6	-0.0	0.1	74.5	3.6***	0.8
US-Mich 437 (4 ×)	C	---	0.6	0.5	---	0.9	0.8	---	-0.2	0.5	---	-1.1	0.7	---	0.1	0.6	---	3.4	4.4
Gorham	C	5.9	0.3*	0.1	7.8	0.4	0.2	7.7	0.8**	0.2	5.4	-0.3	0.2	5.9	0.1	0.2	73.6	3.4***	1.2
Doyenne du Comice	C	---	0.6*	0.2	---	-0.2	0.2	---	0.3	0.2	---	0.1	0.2	---	0.4	0.2	---	3.2	1.5
US 56119-066	CX	6.8	0.3	0.1	6.4	-0.3	0.2	7.4	0.5*	0.1	7.1	0.5	0.2	4.9	0.2	0.2	73.4	3.2	1.3
US 539	C	6.5	0.1	0.1	6.9	0.5***	0.1	6.3	0.4***	0.1	6.1	0.3*	0.1	4.9	-0.0	0.1	70.4	2.9**	0.7
US 309	C	4.8	0.1	0.1	7.2	0.4***	0.1	6.3	0.1	0.1	7.0	0.5***	0.1	6.6	0.4***	0.1	67.3	2.6***	0.5
US 1832	C	3.7	0.2	0.2	5.5	0.4	0.2	5.3	0.2	0.2	4.6	-0.3	0.2	3.5	0.1	0.2	50.0	2.6	1.3
US 56127-003	CX	4.8	0.0	0.2	7.8	0.9	0.3	5.3	-0.3	0.2	6.3	0.6	0.3	5.7	0.4	0.2	65.3	2.4	1.6
US 56112-075	CX	5.2	0.1	0.1	5.8	0.6*	0.2	6.7	0.2	0.2	5.4	0.4	0.2	3.8	-0.4	0.2	61.1	2.3	1.2
US 1753	C	5.9	0.0	0.5	6.4	0.7	0.7	7.5	0.3	0.4	4.6	-0.1	0.7	3.7	-0.2	0.5	66.0	2.3	4.1
US 938	CP	---	0.3	0.1	---	-0.1	0.3	---	0.1	0.2	---	0.3	0.3	---	0.8	0.2	---	2.3	1.6
NJ 5001710820	CP	5.1	-0.2	0.1	6.7	0.6***	0.1	5.8	0.0	0.1	7.8	0.6***	0.1	5.5	-0.1	0.1	65.4	2.2*	0.8
Dawn	C	5.8	0.1	0.1	5.9	0.2	0.1	6.8	0.5***	0.1	6.2	-0.1	0.1	6.0	0.3**	0.1	66.7	2.2*	0.8
US 301	C	5.2	0.2*	0.1	7.2	0.2	0.1	5.8	0.1	0.1	6.4	0.1	0.1	6.1	0.1	0.1	66.7	1.9**	0.7
Miss-US 3-53	C	4.8	0.3*	0.1	5.6	-0.0	0.2	5.1	0.2	0.2	4.5	0.2	0.2	4.4	0.3	0.2	55.1	1.9	1.3
NJ-490871089	CP	5.4	0.2*	0.1	6.3	0.3	0.2	6.7	-0.0	0.1	7.6	0.1	0.2	7.0	-0.0	0.1	68.3	1.7	0.9
Bartlett	C	5.5	0.2*	0.1	6.8	0.2	0.1	6.3	0.1	0.1	6.7	0.3*	0.1	6.8	0.2*	0.1	68.4	1.7**	0.6
US 505	C	5.7	0.0	0.1	6.6	0.4	0.2	5.6	0.3**	0.1	6.5	0.1	0.2	6.5	0.2	0.1	67.0	1.7	0.9
Tenn 34S197	CP	4.2	0.1	0.2	7.3	0.1	0.3	4.7	0.3	0.2	7.0	0.3	0.3	7.3	0.0	0.2	62.5	1.7	1.5
US 521	C	4.6	0.2	0.2	6.7	0.4	0.3	5.2	-0.2	0.2	5.7	-0.6	0.3	5.9	0.5	0.2	60.7	1.4	1.8
US 414	C	4.6	-0.1	0.3	7.0	0.8	0.4	6.1	-0.3	0.3	6.8	0.6	0.4	5.4	-0.4	0.3	63.9	1.3	2.2
NJ 501971234	CP	4.8	0.2*	0.1	6.0	-0.2*	0.1	4.5	-0.0	0.1	8.2	0.9***	0.1	6.1	0.2	0.1	60.2	0.6	0.8
Moonglow	C	4.7	0.1	0.1	7.2	-0.0	0.1	7.3	0.2*	0.1	6.2	0.2	0.1	5.6	0.1	0.1	70.5	0.6	0.6
US 307	C	5.5	0.2*	0.1	5.2	-0.2*	0.1	5.0	-0.2*	0.1	4.7	-0.1	0.1	5.0	0.3***	0.1	57.4	0.4	0.6
US 220	C	4.1	0.2*	0.1	3.0	-1.7***	0.2	4.1	0.2	0.2	4.9	0.6*	0.2	4.6	0.4	0.2	43.2	0.3	1.2
Magness	C	7.1	0.1	0.1	7.3	0.2	0.1	7.4	0.0	0.1	5.3	-0.5***	0.1	5.7	-0.1	0.1	76.1	0.2	0.6
US 447	C	7.1	0.3	0.2	6.9	-0.1	0.3	6.5	0.0	0.2	6.9	-0.3	0.3	7.4	-0.1	0.2	76.5	0.1	1.8
Beurre D'Anjou	C	5.1	0.2	0.1	5.3	-0.1	0.2	5.4	-0.0	0.2	4.7	-0.1	0.2	5.0	0.0	0.2	56.7	-0.1	1.3
Turkey No. 7	X	4.9	-0.2	0.1	6.9	0.4	0.2	5.2	-0.0	0.1	6.6	-0.1	0.2	7.4	-0.3*	0.1	64.5	-0.1	1.0
Pulteney	C	4.6	0.3*	0.1	5.4	-0.6*	0.2	6.8	0.3*	0.1	4.7	-0.1	0.2	4.5	0.6	0.2	57.2	-0.1	1.2
US-Mich 437	C	5.8	-0.2	0.2	6.9	0.2	0.3	5.5	-0.0	0.2	7.0	0.1	0.3	7.0	-0.1	0.2	68.8	-0.8	1.8
US 264	C	3.5	-0.1	0.1	4.8	-0.1	0.1	4.7	0.0	0.1	4.9	-0.5***	0.1	4.2	-0.0	0.1	46.9	-1.3	0.7
US 337	C	5.4	0.0	0.1	5.1	-0.1	0.1	5.5	-0.0	0.1	2.0	-0.5***	0.1	3.2	-0.1	0.1	53.0	-1.3	0.8
US 342	C	4.0	0.1	0.1	5.2	-0.1	0.1	4.3	-0.0	0.1	1.2	-1.0***	0.1	3.1	-0.0	0.1	44.7	-1.4	0.7
Lincoln	C	4.0	0.1	0.2	4.9	-0.9	0.3	4.9	-0.2	0.2	7.0	0.9	0.3	4.7	0.2	0.2	52.3	-1.9	1.8
Seckel	C	5.8	-0.2	0.2	5.2	0.0	0.3	5.6	-0.0	0.2	1.7	-0.8	0.3	1.7	-0.6	0.2	54.8	-2.1	2.0
Richard Peters	CP	3.5	0.0	0.2	5.4	-0.6**	0.2	4.7	-0.0	0.2	4.6	-0.1	0.2	3.4	0.1	0.2	48.0	-2.3	1.3
NJ 5001480202	CP	3.0	-0.2	0.1	3.4	-0.2*	0.1	4.0	-0.3*	0.1	6.6	-0.5***	0.1	5.7	-0.1	0.1	42.4	-2.3*	0.9
Ewart	C	5.1	0.1	0.1	5.0	0.7*	0.2	6.2	-0.1	0.2	4.7	-0.6*	0.2	5.0	0.2	0.2	57.2	-2.8	1.3
Beurre Bosc	C	5.1	0.0	0.2	3.6	-0.1	0.3	4.5	-0.2	0.2	0.2	-1.8**	0.3	6.4	0.0	0.2	47.1	-2.8	1.7
Parberton	C	4.4	-0.3	0.2	6.8	-0.3	0.4	5.6	0.2	0.2	4.4	-0.6	0.3	3.7	-0.6	0.3	57.2	-3.3	2.1
Waite	CP	3.8	-0.2	0.1	4.9	-0.7**	0.2	5.6	-0.2*	0.1	5.3	-0.1	0.1	4.9	0.2	0.1	51.3	-3.3**	0.9
Marie Louise	C	7.5	-0.1	0.2	7.5	-0.6*	0.2	7.9	0.1	0.2	4.2	-0.5*	0.2	6.5	0.0	0.2	79.1	-3.4*	1.3
Old Home	C	3.3	-0.2	0.1	3.5	-0.7***	0.1	3.4	-0.4**	0.1	6.9	0.5***	0.1	3.5	-0.4**	0.1	40.9	-3.8***	0.7

(Continued)

Table 3. continued

Parent	Species	Flavor			Grit			Texture			Russet			Appearance			Weighted total score		
		PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE	PS	GCA	SE
Winter Nelis (4x)	C	---	-0.4	0.5	---	-0.1	0.7	---	0.5	0.4	---	-1.8	0.7	---	-1.6	0.5	---	-4.6	4.0
Kieffer	CP	3.5	-0.5***	0.1	3.6	-1.8*	0.1	4.3	-0.4***	0.1	5.7	-0.3*	0.1	5.2	-0.3**	0.1	44.2	-5.6***	0.4
White Anther	X	3.5	-0.5	0.2	5.5	-1.0	0.4	6.9	-0.4	0.3	7.2	-0.3	0.4	6.5	-0.9	0.3	58.0	-6.6	2.2
US 56112-114	CX	4.1	-0.2	0.1	1.7	-0.9*	0.1	4.1	-0.3*	0.1	2.4	-1.1*	0.1	2.4	-0.4**	0.1	34.7	-6.8***	0.8
Clyde	CX	---	-0.4	0.4	---	-1.1	0.6	---	-0.6	0.4	---	-0.8	0.5	---	-0.2	0.4	---	-7.3	3.2
NJ 487601092	CPU	---	0.6***	0.1	3.8	-1.0***	0.1	---	-1.0***	0.1	---	0.6***	0.1	---	-0.5***	0.1	---	-7.4***	0.6
NJ 5001480917	CP	3.6	-0.4	0.2	6.7	-1.1*	0.3	2.4	-0.9*	0.2	2.4	-2.2**	0.3	3.2	-0.8***	0.1	36.0	-9.7**	1.7
Hansen's Seedling	CU	---	-1.6*	0.3	---	-1.9*	0.3	---	-1.6**	0.2	---	1.0*	0.3	---	-1.1*	0.2	---	-15.8*	2.3
Bradford	CA	---	-2.3***	0.1	---	1.6***	0.2	---	-3.2***	0.2	1.0	-3.1***	0.2	---	-2.2**	0.2	---	-26.2***	1.5

^aCodes for species: C = *P. communis*; P = *P. pyrifolia*; U = *P. ussuriensis*; CA = *P. calleryana*; X = unknown. Interspecific hybrids are indicated by combinations of these species codes.

***, **, *Significant under the null hypothesis ($H_0: g_{i,j} - g_{j,i} = 0$), for a one-tailed *t* test at 5%, 1%, and 0.1%, respectively.

Russet was also of moderately high heritability (0.52), with parental means accounting for half of the variability in progeny means. Among species crosses, the lowest heritability (0.39) was observed within the *P. communis* × unknown subpopulation, while the maximum estimate (0.94) was observed between *P. communis*–*P. pyrifolia* parents. No markedly divergent estimates were observed among other subpopulations involving *P. pyrifolia*, as might have been suggested by the conclusions of Wellington (1913) and Kikuchi (1930), who postulated control by dominant genes. This is probably due, at least in part, to the small number of parents of this ancestry with low russet scores (Table 2). The results agree with those of Hsiong (1938), Crane and Lewis (1949), and Zielinski et al. (1971), all of whom reported that the inheritance appeared to be controlled by several genes.

Appearance had a low heritability for the entire population (0.18) and within species crosses (0.07 for *P. communis* × unknown crosses to 0.38 for *P. communis*–*P. pyrifolia* × unknown crosses). In the context of the breeding program, this trait is a subjective measure of overall visual appeal. Skin finish, shape, russet, color, and, to a lesser extent, size, were considered when assigning scores. The presence of any significance in the heritability may be attributable to the most important component traits; e.g., russet.

The heritability of an index is subject to the heritabilities of the individual component traits. Being composed of three traits of relatively low magnitude, i.e., texture, flavor, and appearance, the heritability of the index was also low ($h^2 = 0.16$). Among the species crosses, the estimates of heritability ranged from nonsignificant for *P. communis* × *P. communis*–*P. pyrifolia* crosses (0.03) to a maximum of only moderate magnitude within *P. communis* × unknown crosses (0.51). The index is, therefore, of little value in selecting parents.

Considerable variability in the heritabilities estimated from the various subpopulations was noted for all traits. Differences may be due, in part, to parents and crosses unique to each group and the effect on the means and variances of the subpopulations. Sampling error may also account for unusually high or low values in subpopulations with few crosses. High values may also indicate parents or species worthy of further examination.

Combining ability. Variances due to both general and specific combining ability were found to be significant for all traits and the weighted index (Table 2). General combining ability effects

were 4.5 (for flavor) to 12 times (for the weighted quality index) greater than SCA effects. The species of the parent appeared to have little effect on the ranking for any quality trait (Table 3). The sole *P. calleryana* cultivar, Bradford, had the lowest constants for russet, texture, flavor, appearance, and weighted total score. 'Hansen's Seedling' had the lowest significant GCA constant for grit. The parents with the highest significant constants were US 56121–008 for flavor, US 725 for grit, 'Gorham' for texture, and NJ 5008710504 for russet, appearance, and total weighted quality. Parents of *P. communis* and interspecific hybrid origin were distributed throughout the range of values.

It is recognized that the unbalanced nature of the parental matings may have introduced some bias into the estimation of SCA, as well as GCA. The nonrandom selection of parents has also probably inflated the variance due to specific combining ability. Of those GCA constants not significantly different from zero, greater confidence should be placed in parental constants with smaller standard errors of the constant. In most cases, constants derived from larger numbers of crosses had the lowest standard errors.

The results indicate that significant, but variable, amounts of additive genetic variance exists for all five fruit quality traits and their weighted total. Several genes, each acting in a primarily additive, but not necessarily equal, fashion, are responsible for the expression of each trait. Selection of parents based on their own phenotypes will result in the most rapid genetic gains for traits of higher heritability, grit, and russet; moderate rates of gain for texture; and low rates of gain for flavor, appearance, and total weighted score. Non-addictive genetic factors (dominance and epistasis), as estimated by SCA, contribute significantly to the total variance of all traits and the weighted index, but at a much lower level than additive genetic factors.

The scoring system used for fruit quality was subjective, rather than objective. A lack of precise definitions for each score must be a source of variability in each of the five traits. However, we are interested in the heritabilities and combining ability constants of the subjective scores, and not directly with the underlying components. The interpretations, therefore, deal with the implications for selection and breeding progress. Efficiency of selection would be improved by making the rating system more objective. More precise definitions of each score relative to standard cultivars might reduce measurement error, thereby in-

creasing the heritability of the scores. Use of the current total weighted score as a selection index is not recommended. Development of a new index to aid simultaneous selection for all traits of interest would be desirable.

The GCA constants may be used to select parents for use in crosses to produce progeny with high-quality fruit. The low magnitude of SCA, relative to GCA, does not warrant the use of progeny testing as an aid to parental selection. The gain in efficiency is not sufficient to compensate for the long juvenile period of pears (usually a minimum of 4 years) and the consequent delay in fruiting. For selection from seedling populations, such an approach is not feasible because of the many crosses and seedlings typical of fruit breeding programs.

A choice of the most efficient selection method depends on the heritability of the trait, the mating design, the phenotypic correlation of family members, and number of seedlings per cross (Falconer, 1981; Lerner, 1958). Precise estimates of relative gain are difficult to estimate for this population, due to variable family size and the unbalanced nature of the mating design. However, data presented by Lerner (1958) suggest that, for traits with a heritability of 0.2 and at least eight progeny per cross, about a 35% gain over individual phenotypic selection would be possible when selection based on individual phenotypic values is supplemented by family means. Lerner (1958) and Falconer (1981) give formulae for determining the weights to be assigned to individual and family deviations when constructing this type of selection index. For decreasing individual heritabilities, family means are given increasingly greater weight. For the range of heritabilities estimated in this study, such combined selection will result in the most efficient and rapid genetic improvement in individual traits. While marginal for grit and russet, the gain in efficiency would be most important to the traits of low heritability, texture, flavor, appearance, and the weighted total score.

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