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Heritability and Phenotypic Correlations of Six Pecan Nut Characteristics

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Abstract. **Heritability estimates for pecan *[Carya illinoinensis* (Wangenh.) K. Koch] nut weight, nut buoyancy, nut volume, nut density, kernel weight, and percentage kernel were determined from 8748 nut samples representing 152 families collected during 25 years in the U.S. Dept. of Agriculture (USDA) pecan breeding program at Brownwood, Texas. Measurements were corrected for year-to-year environmental variability using least-squares constants of individual year effects. Adjusted values were then regressed on midparent means. Generally, heritability (h^2) estimates were low to moderate: nut weight 0.35, nut buoyancy 0.18, nut volume 0.35, nut density 0.03, kernel weight 0.38, and percentage kernel 0.32. The low values are probably due to the extreme alternate bearing tendency of this species, since crop load affects pecan nut characteristics so directly. Phenotypic correlations among these traits showed that larger or heavier nuts had significantly higher kernel weight, buoyancy, and percentage kernel. Nut density increased with higher nut and kernel weight, but decreased with nut volume.**

Pecan genetics remains poorly understood despite its dominant importance in determining the future productivity of this most important native North American nut crop. Novice and professional pecan breeding has been conducted for about a century, resulting in >1000 cultivars (Thompson and Young, 1985). However, only ≈40 cultivars are used commercially (Thompson, 1990). Most selections were based on nut size and quality (thinness of shell, high percentage kernel, and ease of kernel separation from internal packing material).

The Agricultural Research Service, USDA, conducts the only formal pecan breeding program in the world. Data on the performance of hybrids of known parents have been collected by the Brownwood office since 1939. These data have been compiled to estimate heritability of nut characteristics of major economic importance. Heritability estimates are presented here for the first time in scientific literature and provide a basis for parental selection and family size requirements to accomplish different levels of genetic improvement in pecan.

Materials and Methods

The germplasm studied was from the USDA pecan breeding program at Brownwood. It consisted of progenies from controlled crosses routinely made each year to produce improved pecan cultivars. Clones were selected as parents based on yield, nut quality characteristics (size, percentage kernel, or ease of shelling), desirable tree structure, or disease resistance. Crosses were made using the crossing techniques outlined by Smith and Romberg (1940). Seed of known pedigree were planted in the field or greenhouse. During the first summer of growth, buds were taken from each clone and budded into regrowth limbs on bearing pecan trees pollarded (cut back) the previous winter. Seedlings of the same family were usually grouped on one or more mother trees as needed. These mother trees were spaced 10.7 m each way in a square planting design. The buds were forced the following spring and were grown under a high level of orchard management. The juvenile buds normally produced strong and stocky upright trunks so that competition for radiation was relatively uniform. The clones normally fruited the third to fifth leaf (year of growth).

This study includes nut samples collected in 25 of the 41 years from 1945 through 1985. Sixty female and 49 male parents are represented in 152 crosses (reciprocals combined) to give 8748 observations or nut samples. Table 1 presents a breakdown of these samples to show the distribution of years that families were evaluated. The first line shows that for 33 families (crosses), nut samples were collected in only 1 year. Crosses had varying numbers (from one to 3 1) of progeny sampled. Some clones were sampled as many as 12 years (last line of table).

Nut samples of each clone were normally evaluated for three to five seasons to determine if each clone merited further propagation. Basic nut measurements included nut weight and buoyancy. Buoyancy was determined by submerging the sample in water and determining lift in grams. This value was added to nut weight to derive nut volume. The nuts were then shelled and kernel weight was determined.

There was no experiment design with respect to this analysis, since the data were collected initially for other purposes. The methods of data collection do appear to be free of bias, and sufficient numbers were analyzed to provide reasonably accurate heritability (h^2) estimates.

The magnitudes of genotype, year, and genotype × year interactions were evaluated using original data measurements. Since this analysis showed that year effects were large, yearly correction factors were computed, and least-square estimates of year effects were computed to correct the data. The general linear models (GLM) procedure from SAS (1985) was used with a model that included the dependent variable and that considered year effects fixed. Procedures were essentially those described by Hansche et al. (1972b) and given in detail by Henderson (1953). These correction values were appropriately added to or subtracted from

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Abbreviation: h^2, heritability.

Table 1. Number of years pecan nut samples were collected from progeny of various crosses.

Years	No. of families	No. of observations	Minimum no. observations/family	Maximum no. observations/family
1	33	325	1	31
2	33	416	2	90
3	22	684	6	87
4	29	1186	10	133
5	6	199	12	46
6	9	596	17	180
7	5	619	67	192
8	2	333	153	180
9	6	1360	49	563
10	3	454	132	189
11	2	1488	382	1106
12	2	1088	469	619

each sample value. Parental values were averages of data obtained for 5 to 8 years. Linear regression of year-adjusted offspring performance on the average performance of their parents was used to estimate heritability (Kempthorne and Tandon, 1953). Midparent values were repeated for each progeny of each family (Latter and Robertson, 1960). The expectation for the regression of offspring on midparent (b) is the ratio of $V_A : V_P$ or the h^2, where V_A = additive genetic variance and V_P = phenotypic variance. The covariance of offspring and midparent is 1/2 V_A, and the denominator for the offspring and midparent regressron coefficient is 1/2 V_P. This calculation assumes that the contributions of epistatic interactions to covariance are negligible and that the phenotypic variances of the two parental populations are equal. Phenotypic correlations were computed using the progeny measurements after adjustment for year effects.

Results and Discussion

Variance components for genotype, year, and genotype x year interactions generally showed year effects to be very important for the six traits measured (Table 2). Based on that analysis, the decision was made to compute corrections for yearly climate variation.

The range of values among clones for nut weight (after removal of husk) was high (3-10 g/nut). Corrections for year effects (Table 2) indicated high environmental influence associated with measuring this trait. Also, the midparent mean nut weight (7.6 g) was higher than the progeny mean (5.9 g) (Table 3). The reasons for that difference-are not obvious. The h^2 estimate for this trait was 0.35. This value and all other values, except nut density, were significantly different from zero (0.001).

Nut buoyancy (to some extent a measure of air in the nut) ranged from 1.77 g in 1955 to 1.12 g in 1978 (Table 2). Corrections for year-to-year environmental effects were as high as -0.93 g in 1947. Parental values were also higher than progeny values (Table 3), with a low h^2 of 0.18. The value of this trait in a breeding program is debatable. A high buoyancy value may indicate ease of shelling due to space in the nut and between components to separate kernel and shell or packing material; it may also indicate inadequate or small kernel development.

Environmental effects on nut volume were also high, with a maximum correction value of -2.82 ml in 1972. The h^2 of that trait was similar to nut weight and kernel weight. As with nut weight and nut buoyancy, average parental values were higher than progeny values.

Nut density, being a direct function of nut weight and nut volume, showed almost zero h^2. Coefficients of variability also were low for that trait. Therefore, a confounding effect may be present in the data. The above comments concerning buoyancy of pecan nuts also apply to this characteristic to some extent. Bulkiness of pecans, requiring extra storage space, is a minor concern compared to ease of separating the kernel from the shell and packing material. High nut density might, therefore, pose problems for pecan shellers.

Kernel weight is one of the more important characteristics of pecan quality. A strong environmental influence was obvious from relatively high least-square estimates of year effects (Table 2), and the midparent mean was somewhat higher than the progeny mean. The h^2 for that trait was higher than any of the other characteristics studied (0.38), but still much lower than the 0.87 value reported for walnut *(Juglans regia* L.) (Hansche et al., 1972a).

Year-to-year environmental variability of percentage kernel content was lower than that of any other traits (Table 2), yet the heritability was lower than expected. Midparent mean value was close to the progeny mean.

Most phenotypic correlations were highly significant (Table 4). Some correlations were positive and strong (e.g., all comparisons of nut weight, kernel weight, and nut volume). Likewise, nut density was negatively related to nut buoyancy. Larger pecans also tended to be more buoyant (positive relationship between nut volume and buoyancy). Nut buoyancy also increased with nut weight.

Percentage kernel and kernel weight were not as highly correlated as expected, given the fact that kernel weight is used to calculate percentage kernel. Likewise, there was a slight, but significant, association between percentage kernel and nut density, and between percentage kernel and nut weight. All of those values were lower than expected, since the kernel often accounts for more than half of the nut weight.

Some resolution of the debate as to whether larger nuts (measured as volume) were less filled with kernel and perhaps of lower density was apparent from those data. Percentage kernel actually increased slightly with increasing volume, but nut density decreased. Previous research showed both of those comparisons to be negative (Thompson et al., 1989). There appears to be no major genetic problem of maintaining nut density and percentage kernel as nut volume is increased through breeding.

Heritability estimates of additive genetic variance, for all traits, were lower than expected when these data were compared to similar values in Persian walnut. These two crops are similar in many ways (both in the family Juglandaceae), yet are extremely different in fruiting pattern across years. Alternate bearing is not a

Tabler 2. Least-squares means for pecan nut and kernel characteristics (first value) and least-squares estimates of year effects (second value).

		Nut				Kernel	
Year	n	Wt (g)	Buoyancy (g)	Volume (ml)	Density ($g \cdot ml^{-1}$)	wt (g)	Percentage kernel
1945	224	5.89 + 0.97^z	1.71 – 0.26	7.59 + 0.71	0.78 + 0.05	3.51 + 0.33	0.59 – 0.0
1946	57	6.14 – 0.29	1.72 – 0.52	7.84 – 0.80	0.78 + 0.05	3.66 – 0.40	0.59 – 0.04
1947	404	6.11 – 0.66	1.73 – 0.93	7.84 – 1.59	0.77 + 0.10	3.69 – 0.51	0.60 – 0.02
1950	74	5.03 + 0.33	1.46 – 0.68	6.49 – 0.35	0.78 + 0.10	3.16 – 0.17	0.56 + 0.00
1955	110	5.85 + 1.82	1.77 – 0.52	7.62 + 1.30	0.76 + 0.10	3.13 + 0.76	0.54 – 0.03
1959	73	5.89 + 0.62	1.19 – 0.27	7.08 + 0.35	0.83 + 0.05	3.40 + 0.45	0.58 + 0.02
1961	310	5.39 + 0.33	1.53 – 0.28	6.92 + 0.05	0.78 + 0.04	3.04 + 0.30	0.56 + 0.02
1962	56	5.19 + 0.95	1.53 – 0.44	6.72 + 0.51	0.77 + 0.08	2.95 + 0.61	0.56 + 0.02
1967	62	6.71 – 0.12	1.35 – 0.40	8.07 – 0.53	0.84 + 0.04	3.80 – 0.10	0.57 – 0.01
1968	442	6.76 – 0.56	1.39 – 0.31	8.16 – 0.87	0.83 + 0.03	3.86 – 0.24	0.57 + 0.01
1969	827	6.96 – 1.03	1.42 – 0.39	8.38 – 1.42	0.82 + 0.03	3.96 – 0.69	0.57 – 0.02
1970	1439	6.71 – 1.21	1.34 – 0.54	8.05 – 1.75	0.84 + 0.04	3.83 – 0.65	0.57 + 0.01
1971	472	6.73 – 0.59	1.37 – 0.12	6.67 + 0.71	0.84 + 0.00	3.83 – 0.14	0.57 + 0.03
1972	801	6.79 – 2.05	1.35 – 0.78	8.13 – 2.82	0.90 + 0.06	3.83 – 1.16	0.56 + 0.00
1973	1019	6.92 – 1.09	1.36 – 0.43	8.26 – 1.51	0.83 + 0.03	3.90 – 0.57	0.56 + 0.01
1974	34	6.70 + 0.13	1.27 + 0.18	7.95 + 0.32	0.85 – 0.02	3.65 + 0.15	0.54 + 0.01
1975	306	6.89 – 0.31	1.38 – 0.09	8.28 – 0.41	0.83 + 0.01	3.90 – 0.07	0.56 + 0.02
1976	301	6.59 – 0.66	1.29 – 0.38	5.81 + 1.04	0.84 + 0.03	3.69 – 0.42	0.56 – 0.01
1977	173	6.45 – 0.97	1.29 – 0.07	7.75 – 1.04	0.84 – 0.02	3.57 – 0.58	0.55 – 0.01
1978	65	6.02 – 0.74	1.12 – 0.27	7.14 – 1.01	0.84 + 0.02	3.26 – 0.39	0.54 + 0.00
1979	665	6.10 + 0.48	1.44 + 0.08	7.54 + o.56	0.81 + 0.00	3.46 + 0.31	0.56 + 0.01
1981	29	6.55 + 0.28	1.21 + 0.40	7.76 + 0.68	0.885 – 0.04	3.59 –0.13	0.54 – 0.04
1983	6	6.41 – 0.83	1.22 – 0.10	7.63 – 0.93	0.84 – 0.00	3.53 – 0.33	0.55 + 0.02
1984	175	6.49 + 0.47	1.21 + 0.01	7.69 +0.48	0.84 + 0.01	3.60 + 0.27	0.56 + 0.00
1985	634	6.46^y	1.15	6.93	0.86	3.36	0.57
Overall Mean	350	5.90	1.02	6.93	0.86	3.36	0.57

[z] Least-squares estimates of year effects.

[y] The solution matrix for the model is not of full rank and, therefore, a generalized inverse was employed to arrive at a solution. The effect in the last row and column cannot be estimated.

problem in walnut (McGranahan and Leslie, 1991), but is a major problem in pecan (Thompson and Grauke, 1991). The effects of alternate bearing is a major source of error when determining the nut quality characteristics studied here. This is true since heavy nut set on a tree often results in poorly filled nuts (overbearing), while a light nut set results in extremely well-filled nuts of high quality. Also, the effects cannot be addressed statistically, since variance is across years, and trees are not synchronized in a test, as reported here.

Although heritability may be relatively low for the nut characteristics in pecan studied here, especially when compared to some other nut species, values of 0.3 or higher are sufficient to produce significant breeding improvement. For instance, selection response can be estimated by heritability x selection differential to give response per generation. The phenotypic SD for nut weight was estimated to be 1.46 g and heritability was 0.35. Therefore, selection response per generation, if parents were selected from those one SD above the mean, would result in an increase of ≈0.5 g/generation. This is a valuable genetic improvement and is genetically fixed in pecan, since only vegetative propagation is used in testing and orchard establishment.

There also seems to be a particularly high level of nonadditive genetic control for some of the traits studied. These data may contain subsets that could be partitioned out to further define nonadditive effects, but this further partitioning could not increase the accuracy of these h^2 estimates. This is true since the estimation of narrow-sense h^2, as determined here, only requires partitioning additive genetic variance in relation to all other effects.

Table 3. Estimates of midparent means, progeny means, and h^2 of six pecan traits

	Midparent		Progeny		h^2		Phenotypic SD
Trait	Mean	CV^z	Mean	CV	Estimate	CV	(g)
Nut wt (g)	7.58	16.2	5.90	24.7	0.35	20.4	1.46
Nut buoyancy (g)	1.81	35.9	1.02	52.9	0.18	34.2	0.54
Nut vol (ml)	9.39	18.7	6.93	26.0	0.35	19.3	1.80
Nut density ($g \cdot ml^{-1}$)	0.82	3.7	0.86	7.0	0.03	6.8	0.06
Kernel wt (g)	4.20	16.0	3.36	26.5	0.38	22.2	0.89
Percent kernel	0.56	5.4	0.57	8.8	0.32	7.8	0.05

[z] CV = coefficient of variability.

Table 4. Correlations among phenotypic characteristics of pecan nuts. All correlations were significant ($P \leq 0.002$, df = 8747).

Trait	Kernel content (%)	Nut density ($g \cdot ml^{-1}$)	Nut volume (ml)	Kernel wt (g)	Nut buoyancy (g)
Nut wt (g)	0.104	0.116	0.962	0.952	0.378
Nut buoyancy	–0.033	–0.852	0.617	0.348	
Kernel wt (g)	0.394	0.123	0.912		
Nut volume (ml)	0.079	–0.155			
Nut density ($g \cdot ml^{-1}$)	0.098				

Major genes increase h^2, but perhaps their effect in this study was minor, since crosses should have been random in regard to presence or absence of these genes (free of assortive mating). Epistatic gene action is assumed to be zero here, although additive × additive effects increase the h^2 estimates. The parent-offspring regression technique is the least biased technique to use in these calculations. Also, by definition, dominance variation reduces narrow-sense h^2 but not broad-sense h^2. All these factors lower the predictability of offspring performance using parental values. At the same time, genetic improvement in the USDA breeding program continues as clones are identified with adequate nut size and other quality traits (T.E. Thompson, unpublished data). Perhaps this improvement is due to the efficiency of detecting genetically stable differences among progeny after clones are vegetatively propagated.

These results also indicate that the new clonal evaluation system of initially growing a tree from seed and allowing uniform space for tree development should improve the ability to distinguish among clones. A major improvement here will be the ability to follow individual clone (tree) performance by age under uniform culture across years.

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