Provenance Variation in Pecan

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ABSTRACT. An assessment of vegetative traits of pecan [*Carya illinoensis* (Wangenh.) K. Koch] from a range-wide provenance collection indicated the existence of at least two distinct populations within the native range (i.e., provenances north of Texas vs. provenances in Texas and Mexico). Southern most provenances generally broke bud earlier, retained foliage later in the fall, grew larger in height and trunk diameter, had narrower leaflet droop angles, had greater leaflet tilt angles, wider limb angles, greater Zn deficiency, less black pecan aphid susceptibility, and less red coloration to foliage than did northern most provenances. Trees originating from Jaumaua, in northern Mexico, were especially noteworthy inasmuch that they were by far the tallest, possessed the largest trunk diameters, the longest foliation period, and lowest Zn deficiency ratings of all provenances. One family within this Jaumaua population also exhibited a high level of cold hardiness. Family heritability (h^2) estimates were ≥ 0.48 for trunk cross sectional area, date of budbreak, leaf redness, cold injury, leaflet droop angle, and leaflet tilt angle, and ≤ 0.39 for late season leaf fall, black pecan aphid susceptibility, zinc deficiency, and branch angle.

Pecan [*Carya illinoensis* (Wangenh.) K. Koch], a silvicultural crop (Fowells, 1965), has also become a horticultural crop (Flack, 1970; Wood et al., 1990). Its native range appears to extend discontinuously from northern Iowa (42° 20' N. Lat.) in the United States to the vicinity of Oaxaca (16° 30' N. Lat.) in southern Mexico (Thompson and Grauke, 1991) where it grows along the floodplain of the Mississippi, Ohio, Arkansas, Illinois, Missouri, Nueces, Colorado, Brazos, Trinity, and Red Rivers and their tributaries and in isolated pockets along the small rivers of central and southern Mexico (Fowells, 1965).

An understanding of natural variation patterns is important for improvement of crops (Bagley, 1980). Pecans' natural range is large, spanning 26° in latitude, but generally discontinuous with many isolated populations (Thompson and Grauke, 1991). Therefore, there is likely substantial genetic diversity (Wright, 1976). This study assesses geographic variation patterns within the natural range for horticulturally important traits (height and diameter growth, time of budbreak and leaf fall, leaf redness, cold injury, black pecan aphid susceptibility, zinc deficiency, foliar display angles, and branch angle), identifies superior provenances and families, provides heritability estimates of these traits, and provides insight into major subgroups within the native range.

Materials and Methods

Nuts were collected in 1986 and 1987 from wild pecan trees at 19 distinct source locations, or provenances, ranging from northern Missouri in the United States to Oaxaca in Mexico (Table 1). Nuts from five randomly chosen trees, separated as far apart as

practical (ranging from ≈ 50 m to 10 km, but usually >200 m with several wild pecan trees between source trees) were sampled to reflect the genetic nature of each provenance. Nuts were germinated in a greenhouse and planted in the field, on a good pecan site [on a Faceville Sandy Loam soil (siliceous thermic Typic Paleudult)], in March 1989 at a 6-m equilateral spacing. The experimental design was treated as completely randomized with 10 seedlings from each maternal parent [(i.e., replications consisted of single trees from each of the five families within each of the 19 provenances ($n \approx 950$ trees planted at random))]. Fertilizers were applied according to Georgia Extension Service recommendations (Ellis et al., 1995) and transplants were irrigated the first growing season. Weeds were controlled by herbicides and mowing.

Several important vegetative traits were measured after 7 years of growth in the field (1996). Tree height (taken in March from ground to tip of tallest limb) and trunk cross sectional area (calculated from circumference taken 30 cm above the ground in March) provided a characterization of tree size.

Limb angle (average angle between the four lowest scaffold limbs and the trunk) and leaflet droop and tilt angles provided a characterization of canopy structure. Sampling of four compound leaves in mid August from the exterior of the lower one-third of the southern exposed canopy provided estimates of leaflet droop and tilt angles. Droop angle is the angular distance between the abaxial planes of opposite leaflets at the center of the compound leaf (i.e., relatively flat compound leaves produce large angles whereas relatively narrow angles reflect drooping leaflets that produce a rib cage-like appearance). Leaflet tilt angle is the angular distance the plane of the base of leaflets project above the plane of the rachis of the compound leaf to which the leaflet is attached (i.e., small angles reflect a nearly flat compound leaf whereas large angles reflect a window shutter-like appearance). Measurements of leaflet droop and tilt came from the same leaflets.

Winter cold injury occurred in January 1996 (-12 °C) with

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damage being rated in May. A visual survey of damage led to the use of the following damage rating scale: 1 = 0% of shoots within the canopy killed, 2 = 2% to 5% of shoots killed, 3 = 6% to 25%, 4 = 26% to 50%, and 5 = 51% to 100% of shoots within the canopy killed).

Foliar susceptibility to zinc deficiency and black pecan aphid [*Melanocallis caryaefoliae* (Davis)] feeding damage was assessed in 1995–97. Foliar zinc deficiency symptoms were also rated on a scale of 1 to 5 (1 = no deficiency, 2 = wavy leaf margins, 3 = slight interveinal chlorosis of leaflets, 4 = heavy interveinal chlorosis of leaflets, 5 = interveinal necrosis of leaflets and/or dead shoots) in July 1996 and 1997 (Goff et al., 1989). Late-season black pecan aphid damage was rated in September 1995 and 1996 (1 = no black aphid damage, 2 = 1% to 5% of compound leaves exhibiting chlorotic blotches due to aphid feeding, 3 = 6% to 25% exhibiting blotches, 4 = 26% to 50% exhibiting blotches, 5 = 51% to 100% of leaves with aphid induced chlorotic blotches) (Goff et al., 1989).

Foliar budbreak, leaf drop, and coloration was assessed in 1993–98. Date of budbreak (defined as date of first appearance of inner bud scale split on the exterior canopy) and degree of leaf fall (percentage of leaflets on 10 randomly selected compound leaves from the lower exterior of the canopy missing on 15 December) were rated in 1993–95. Red coloration of foliage was rated in July, ≈4 months after budbreak, 1996 and 1997, on a scale of 1 to 5 (1 = green or no reddish tint, 2 = trace of red, 3 = faintly red, 4 = moderately red, 5 = dark red). Sampled leaves were from the lower exterior of the canopy.

Variability and nature of population differentiation were estimated via analysis of variance (SAS Institute, Cary, N.C.). Trees within a family were assumed to be half-sibs because selfing in maternal trees was unlikely due to the general separation of male and female flower maturity windows in pecan (Wood, 1997) and are assumed to possess a different pollen parent due to the abundance of possible pollen sources near the maternal parent. Because the ANOVA was structured to allow for unequal replications due to tree death (Huntsberger and Billingsley, 1973) the ANOVA for

each trait slightly differed; however ANOVAs were partitioned into provenance ($df = P - 1$; $EMS = \sigma^2 + n_1\sigma_r^2 + Q_p$), family (provenance) ($df = P(F - 1)$; $EMS = \sigma^2 + n_0\sigma_f^2$), and error ($df = N - PF$; $EMS = \sigma^2$), where P = number of provenances, N = total number of single tree plots in the planting, F = number of families in each provenance, n_1 = number of replications for each provenance $\times$ family, and $n_0 = (P(F - 1))^{-1}(N - N^{-1}\sum n_p^2)$. This same general form was used in the calculation of family (h_f^2) and single tree (h_t^2) heritability and standard error ($\sigma_{h_f^2}$, $\sigma_{h_t^2}$) estimates using the restricted maximum likelihood method. Family heritabilities and standard error ($\sigma_{h_f^2}$) were estimated using the equation $h_f^2 = \sigma_f^2 / (\sigma_e/r) + \sigma_r$, and $\sigma_{h_f^2} = (1 - h_f^2/4)(1 + (r)h_f^2/4)/n_0[(F - 1)/2]^{1/2}$. Individual tree heritabilities (h_t^2) and standard errors ($\sigma_{h_t^2}$) were estimated using the equation $h_t^2 = 4\sigma_f^2/\sigma_r + \sigma_e$, and $\sigma_{h_t^2} = (1 - h_t^2/4)(1 + (r)h_t^2/4)/[r(F - 1)/2]^{1/2}$ (Wright, 1976). These estimates assume that trees within families are half-sibs. While it is theoretically possible that a few individuals may be full-sibs, the natural separation of male and female flower maturity within maternal trees coupled with the generally large number of adjacent candidate trees as likely pollen sources, justifies half-sib analysis as a reasonable means of estimating heritability. It should be noted that since it was not possible to test provenances at multiple sites, it is impossible to determine environmental variation, thus heritability estimates are likely to be slightly high. Such shortcut techniques are commonly used in forestry and usually result in only slight overestimates of heritability while providing valuable insight into the potential for genetic gain (Wright 1976).

Scott-Knott cluster analyses (Scott and Knott, 1974; Willavize, et al., 1980; Gates and Bilbro, 1978) separated family and provenance groupings for vegetative variables and location factors (i.e., precipitation, elevation, annual minimum and maximum temperatures) into groupings of similarity. Correlation and stepwise multiple regression analyses were used to detect relationships and to identify variables most associated with observed variation. Variables were standardized to zero mean and unit variance before analysis since they possessed different dimensionalities. A variety

Table 1. Location, elevation, and climatic indicators of pecan provenances from throughout the native range.²

No.	Country	State	County	Code	Lat.	Elevation (m)	Precipitation (cm·yr ⁻¹)	Mean temp (°C) ³	Temp range (°C) ³	Min temp (°C) ³
1	U.S.	Missouri	Livingston	Mo-L	39°50'	213	89	12.4	26.4	-23 to -26
2	U.S.	Illinois	Jersey	Il-J	39°00'	192	90	11.4	24.9	-23 to -26
3	U.S.	Missouri	Vernon	Mo-V	37°50'	226	100	13.9	25.6	-21 to -23
4	U.S.	Kentucky	Webster	Ky-W	37°30'	125	111	13.8	25.1	-21 to -23
5	U.S.	Kansas	Cowley	Ks-C	37°20'	347	80	14.6	25.7	-21 to -23
6	U.S.	Kansas	Cherokee	Ks-K	37°00'	274	100	14.3	25.6	-21 to -23
7	U.S.	Tennessee	Lake	Tn-L	36°20'	94	122	14.8	26.1	-18 to -20
8	U.S.	Texas	Bowie	Tx-B	33°33'	119	113	17.1	22.7	-9 to -12
9	U.S.	Mississippi	Washington	Ms-w	33°53'	39	132	17.4	23.0	-9 to -12
10	U.S.	Texas	Tom Green	Tx-T	31°22'	580	46	18.7	21.1	-12 to -15
11	U.S.	Texas	Val Verde	Tx-V	30°00'	313	44	21.0	19.1	-7 to -9
12	U.S.	Texas	Gonzales	Tx-G	29°30'	95	98	19.8	19.2	-7 to -9
13	U.S.	Texas	Kinney	Tx-K	29°14'	227	54	21.9	19.0	-7 to -9
14	U.S.	Texas	Zavala	Tx-Z	28°53'	341	54	21.0	19.8	-4 to -7
15	Mexico	Tamaulipas	Jaumave	Mx-J	23°22'	884	75	24.4	11.8	-1 to -4
16	Mexico	S.L.P.	Santa Clara	Mx-C	22°04'	1219	36	17.9	7.8	-1 to -4
17	Mexico	Hidalgo	Ixmiquilpan	Mx-I	20°29'	1829	39	14.2	4.3	2 to -1
18	Mexico	Jalisco	Sayula	Mx-S	19°55'	1372	90	19.1	8.0	4 to 2
19	Mexico	Oaxaca	Oaxaca	Mx-O	17°05'	1737	64	20.6	5.1	4 to 2

²For the United States, NOAA, 1986. For Mexico, Garcia de Miranda et al., 1980.

³Mean annual temperature, range and minimum temperatures from USDA Plant Hardiness Zone Map.

of multivariate cluster analysis methods (Average Linkage, Complete Linkage, Centroid Hierarchical, Equal Variance Maximum Likelihood, and Ward's Minimum Variance Cluster Analysis) were used for identification of major provenance groupings within the natural range (SAS Institute).

Results

All traits investigated in this study varied in a nonrandom manner (at $\alpha \leq 0.05$) among provenances and among families within provenances.

TEMPORAL ASPECTS OF FOLIATION. Budbreak varied among provenances and within families (Table 2). Range among provenances was 25 d, from 12 Mar. (calendar date 71 for Mx-J) to 6 Apr. (calendar date 96 for Ks-C). Scott-Knott Cluster Analysis partitioned the provenances into four classes with southern sources breaking bud earlier in the spring than northern sources. Stepwise multiple regression analyses (SMRA) of location variables, with latitude held in the model, show budbreak as possessing a negative association with maximum temperature ($R^2=0.17$; Tables 3 and 4).

Leaf fall in December differed among provenances and families (Table 2) such that southern sources (correlation in Table 3) retained foliage far later in the fall than northern sources (i.e., drop was 49% for Mx-I vs. 99% for Mo-L). Many Mexican sources retained substantial green foliage until mid January, whereas many northern seedlings had dropped leaves by early November. SMRA indicated that precipitation, temperature and elevation were unrelated to leaf fall (Table 4).

Trees of all provenances and families exhibited red coloration by foliage, rachis, and shoot tissues. Northern sources tend to be

redder than southern sources ($r = 0.47$; Tables 2 and 3). SMRA showed redness was unrelated to precipitation, temperature, and elevation characteristics (Table 4). Darkest red foliage was from Kansas sources whereas the least degree of redness appeared from Sayula, Mexico, sources (Table 2).

SPATIAL ASPECTS OF FOLIATION. Provenances vary in leaflet droop angle with some possessing wide (flatten appearance) and others narrow angles (ribcage-like appearance; Table 2). Southern sources exhibited narrower angles (Tables 2 and 3) with latitude accounting for 49% of the variation, although precipitation (24%) and maximum temperature (10%) also accounted for significant variability (Table 4). Angular distance spanned 97° [65° (ribcage-like) for the Mx-C #3 family to 162° (flattened or horizontal-like) for the Ky-W #4 family]. Compound leaves with large droop angles (i.e., flat leaves) possess leaflets exhibiting greater leaflet tilt angles (i.e., shutter-like appearance) ($r = 0.66$; Table 3). These leaflet tilt angles spanned 30° [27° (nearly closed shutter-like appearance) for the Mx-C #3 family to 57° (open shutter-like appearance) for the Tx-B #4 family] (Table 2).

Latitude accounted for 30% of the variation in limb angles and precipitation accounted for 10% of the variation (Table 4). Limb angles are not associated with temperature or elevation (Table 4). Limb angles diminished as latitude increased (Tables 2 and 3). Provenances separated into two limb angle classes exhibiting mean angular differences of only $\approx 5^\circ$ (Table 2). Texas and Mexico sources generally exhibited wider angles than other provenances. The greatest limb angle was 61° , exhibited by Tx-K #1, whereas the narrowest was 42° , exhibited by Ky-W #2.

TREE SIZE AND COLD INJURY. Mean height of 7-year-old seedling trees from provenances differ by $\approx 100\%$, ranging from 2.5 m for

Table 2. Means from Scott-Knott univariate cluster analysis of vegetative characteristics for pecan provenances.

Provenance ¹	Budbreak ² (date)	Leaf fall ³ (%)	Tree ht (m)	Trunk area (cm ²)	Zinc deficiency ⁴ (rating)	Aphid resistance ⁵ (rating)	Red color ⁶ (rating)	Cold injury ⁷ (rating)	Leaflet droop angle (°)	Leaflet tilt angle (°)	Limb angle (°)
Mo-L	93 d	99 f	2.5 a	22 a	1.6 a	3.8 c	4.2 b	1.2 a	135 b	50 c	50 a
Il-J	93 d	98 f	3.0 a	34 a	1.7 a	4.2 d	4.1 a	1.2 a	142 b	53 d	50 a
Mo-V	93 d	97 f	3.5 b	44 a	1.9 b	3.9 d	4.5 b	1.2 a	143 b	47 c	52 a
Ky-W	94 d	96 f	2.7 a	26 a	1.8 a	3.5 b	3.8 a	1.5 a	139 b	50 d	48 a
Ks-C	96 d	96 f	3.0 a	35 a	1.7 a	4.0 d	4.5 b	1.3 a	135 b	48 c	51 a
Ks-K	94 d	96 f	3.3 b	40 a	2.0 b	3.6 c	4.6 b	1.6 a	138 b	46 c	54 b
Tn-L	93 d	95 f	3.3 b	41 a	1.6 a	3.7 c	4.0 a	1.3 a	144 b	53 c	51 a
Tx-B	94 d	90 e	3.5 b	47 a	2.1 b	4.1 d	4.2 b	1.1 a	134 b	49 c	54 b
Ms-W	90 d	84 d	4.2 c	62 b	2.1 b	3.3 b	4.2 b	1.4 a	148 b	52 c	52 b
Tx-T	85 c	93 e	3.2 b	42 a	2.6 c	3.6 c	4.1 a	1.3 a	122 a	43 b	53 b
Tx-V	81 b	91 e	3.1 b	33 a	2.7 c	3.5 b	4.0 a	1.5 a	110 a	38 a	54 b
Tx-G	77 b	69 c	4.4 c	93 c	2.4 c	2.9 a	3.9 a	1.4 a	135 b	45 c	52 a
Tx-K	80 b	90 c	3.3 b	57 a	2.6 c	3.8 c	4.2 b	1.5 a	117 a	39 a	55 b
Tx-Z	79 b	82 d	4.3 c	71 b	2.9 d	3.5 b	3.8 a	1.7 a	122 a	43 b	53 b
Mx-J	71 a	50 a	4.9 c	111 c	2.6 c	3.3 b	4.2 b	2.8 c	125 a	38 a	54 b
Mx-C	82 c	62 b	4.1 c	78 b	2.8 d	3.1 a	3.9 a	2.6 c	125 a	39 a	52 b
Mx-I	81 b	49 a	4.0 c	79 b	2.9 d	3.1 a	4.1 a	2.4 b	126 a	39 a	55 b
Mx-S	80 b	69 c	3.1 b	37 a	2.9 d	3.0 a	3.6 a	2.9 c	121 a	43 b	52 a
Mx-O	78 b	60 b	4.0 c	92 c	2.9 d	3.2 a	4.0 a	2.0 b	113 a	43 b	53 b

¹Days into the calendar year.

²Percentage of leaves missing on 15 Dec.

³Zinc deficiency where 1 = no deficiency, 2 = wavy leaf margins, 3 = slight chlorosis of leaflets, 4 = heavy chlorosis of leaves, 5 = necrosis of leaves and/or dead shoots.

⁴Black aphid resistance where 1 = no black aphid damage, 2 = 1% to 5% of compound leaves exhibiting chlorotic blotches due to aphid feeding, 3 = 6% to 25% exhibiting blotches, 4 = 26% to 50% exhibiting blotches, 5 = >50% of leaves with aphid induced chlorotic blotches.

⁵Red coloration of leaf where 1 = green or no reddish tint, 2 = trace of red, 3 = faintly red, 4 = moderately red, 5 = dark red.

⁶Shoot death at 0% = 1, at 1% to 5% = 2, at 6% to 25% = 3, at 26% to 50% = 4, and at >50% = 5.

⁷Ranked from highest to lowest northern latitude.

Table 3. Pearson correlative coefficients (r) for pecan vegetative traits with environment and location variables at sources of origin.

Trait	Lat. and environmental parameters				
	Latitude	Precipitation	Max Temp	Min Temp	Elevation
Budbreak	0.82 ^{***}	0.59 ^{**}	-0.84 ^{***}	-0.84 ^{***}	-0.54 ^{**}
Leaf fall	0.89 ^{***}	0.41 ^{NS}	-0.52 [*]	-0.86 ^{***}	-0.80 ^{***}
Tree height	-0.61 [*]	-0.22 ^{NS}	0.64 [*]	0.66 [*]	0.33 ^{NS}
Trunk area	-0.70 ^{***}	-0.31 ^{NS}	0.63 [*]	0.72 ^{***}	0.47 [*]
Zinc deficiency	-0.90 ^{***}	-0.70 ^{***}	0.75 ^{***}	0.93 ^{***}	0.69 ^{**}
Aphid resistance	0.74 ^{***}	0.26 ^{NS}	-0.46 [*]	-0.74 ^{***}	-0.60 ^{***}
Red coloration	0.47 [*]	0.21 ^{NS}	-0.29	-0.50 [*]	-0.33 ^{NS}
Cold injury	-0.83 ^{***}	-0.42 ^{NS}	0.44 ^{NS}	0.76 ^{**}	0.81 ^{***}
Leaflet droop angle	0.70 ^{***}	0.80 ^{***}	-0.71 ^{***}	-0.69 ^{**}	-0.54 ^{**}
Leaflet tilt angle	0.72 ^{**}	0.83 ^{***}	-0.69 ^{**}	-0.71 ^{**}	-0.58 ^{NS}
Limb angle	-0.55 [*]	-0.50 [*]	0.62 ^{***}	0.63 ^{**}	0.33 ^{NS}
Latitude	---	0.56 ^{**}	-0.63 ^{**}	-0.96 ^{***}	-0.87 ^{***}

NS, *, **, *** Nonsignificant or significant at $\alpha \leq 0.05$, 0.01, or 0.001, respectively.

Mo-L to 4.9 m for Mx-J (Table 2). Height for families ranged from 1.3 m for Mx-C #3 to 5.7 m for Mx-J #2. Similar differences occur for trunk cross sectional area. The largest trees originated from Jaumave (Mx-J), an isolated desert region in northeastern Mexico (Fig. 1). These trees also exhibited the longest foliation period of all provenances and relatively low cold hardiness, although one family from Jaumave exhibited essentially no cold injury. The average minimum temperature for the Mx-J provenance is -1°C (Table 1). These data indicate that the Mx-J gene pool likely contains genes for cold tolerance and rapid growth.

The test location was exposed to winter temperatures of about -12°C during January 1996. Trees from several sources exhibited cold injury to shoots. Degree of cold injury was inversely related to latitude and was unrelated to precipitation, maximum or minimum temperature, and elevation (Table 4). Northern sources exhibited little, or no, cold injury whereas southern sources generally exhibited substantial injury (Table 2); however, one family from the fast growing Mx-J provenance (Mx-J #4) exhibited little or no cold injury.

FOLIAR HEALTH TRAITS. Trees originating from Mexico tend to exhibit greater zinc deficiency, except that those from the fastest growing provenance (Mx-J) exhibited less deficiency than other Mexican sources (Table 2). Precipitation and minimum temperature individually accounted for $\approx 6\%$ of the variation in zinc

deficiency (Table 4). Source trees in Mexico and Texas were on neutral to alkaline soils (pH 7 to 8) whereas northern sources were acidic (pH 6 to 7), as was the test site (pH 6.6). Zinc deficiency was essentially absent in the relatively slow growing families (Mo-V #1 and Tn-L #2). Since foliar Zn levels are influenced by growth rate, it is possible that the absence of deficiency in certain test trees is due to growth rather than uptake efficiency or physiological use.

Black aphid damage to foliage, as determined by the number of chlorotic blotches, was evident for all families and provenances (Tables 2 and 3). Northern sources tend to sustain greater damage than southern locations (Table 3); thus, Mexican sources exhibited less damage than other sources. Least damage (rating of 2.0) was from the Mx-O #4 family (from Oaxaca, Mexico) whereas greatest damage (rating 4.75) was from Il-J #5 (from Illinois). The test planting appeared to have been uniformly (except for specific genotypes) populated by black aphids.

HERITABILITIES. The evaluation of trees at a single site means the genotype-environment interaction cannot be separated from genetic variation among families and individuals, thus slightly overestimating heritability (Wright 1976). Family and single tree heritability estimates were relatively high for most vegetative traits (Table 5), indicating substantial genetic variation potential for selection and improvement in these traits. Budbreak, tree height, trunk cross sectional area, and cold injury appear to be highly heritable.

Table 4. Partial regression coefficients for stepwise multiple regression equations for vegetative traits of pecan with environmental variables. Latitude was the first variable entered and was held in the model.^z

Trait	Partial R^2					
	Total R^2	Latitude	Precipitation	Max temp	Min temp	Elevation
Budbreak	0.84	0.67	NS	0.17	NS	NS
Leaf fall	0.80	0.80	NS	NS	NS	NS
Tree height	0.54	0.37	NS	NS	NS	0.17
Trunk area	0.56	0.48	NS	NS	NS	0.08
Zinc deficiency	0.94	0.82	0.06	NS	0.06	NS
Aphid resistance	0.55	0.55	NS	NS	NS	NS
Red color	0.22	0.22	NS	NS	NS	NS
Cold damage	0.69	0.69	NS	NS	NS	NS
Branch angle	0.54	0.30	0.10	NS	0.14	NS
Leaflet drop angle	0.83	0.49	0.24	0.10	NS	NS
Leaflet tilt angle	0.86	0.52	0.27	0.07	NS	NS

^zAll variables in the model are significant at the $P \leq 0.15$.

Fig. 1. The apparent native distribution of pecan. Numbers refer to provenance collection sites identified in Table 1.

CLUSTER ANALYSIS OF VEGETATIVE TRAITS. Complete Linkage Cluster Analysis indicated the existence of at least two distinct populations within the native range of pecan. One encompasses provenances north of Texas and the other encompasses provenances in Texas and Mexico. The exception is that the Tx-B population is aligned with the northern population.

Discussion

The observation that southern sources break bud earlier in the spring than northern sources support the same conclusion from a relatively small sampling within Oklahoma (Harris and Tauer, 1987). This characteristic appears to be atypical of most North American trees (Wright, 1976), although it is also exhibited by *Juglans nigra*, a relative of pecan (Bey, 1973).

Most Mexican sources retained green foliage until mid January, whereas foliage of northern sources had dropped by early November. Thus, southern sources display foliage for a far greater period during the growing season than do northern sources. This suggests that southern sources may possess greater potential for seasonal photoassimilation. This prolonged foliation raises questions concerning the nature of the interaction between alternate bearing and leaf retention. Worley (1979 a, 1979b) demonstrated that, within a genotype, the retention of healthy foliage after fruit ripening enhances the subsequent crop. This has led to speculation that, regardless of genotype, trees ripening their crop early (exhibiting a relatively long time between ripening and leaf fall) will generally exhibit little or no alternate bearing (Monselise and Goldschmidt, 1982). Observations of parent trees suggest otherwise inasmuch that during nut collection we noted that crop load ("on" vs. "off") of trees within targeted stands exhibited no indication of north-south differences in the frequency of bearing vs. nonbearing trees. Subsequent questioning of residents local to extreme southern provenances revealed that such trees also exhibit severe alternate bearing, although most retain healthy foliage for as much as ≈ 2 to 3 months longer after fruit ripening than do northern trees. Therefore, while stable bearing within a specific genotype is likely

diminished by retention of foliage after nut ripening, it does not ensure stable bearing. Thus, breeding strategies to overcome alternate bearing cannot solely focus on early ripening, but must also consider other bearing related criteria (Grauke and Thompson, 1996; Reid et al., 1993; Smith et al., 1986; Wood, 1995).

Assimilation of information from residents local to source trees indicated that fruit ripening in southern sources is earlier in the season and more protracted than northern sources. While the apparent earlier ripening of southern sources would likely aid marketing of the crop (Wood, 1993), the ≈ 4 weeks protraction of the ripening period by southern sources would tend to be a disadvantage due to potential loss in nut quality and increased harvesting costs (Kays, 1991).

The prominence of red colored foliar tissues by northern sources suggests potential for the development of genotypes useful for ornamental purposes. This coloration is especially pronounced in Kansas and Missouri sources. This positive association with higher latitudes is opposite to that in black walnut (*Juglans nigra*), a distant relative (Bey, 1973).

The large differences in daylength and precipitation characteristics between southern and northern provenances and the associated differences in foliar architecture indicate that limb angles, leaflet droop angles and leaflet tilt angles may confer an adaptive advantage to trees in these diverse environments. Because foliar angles affect light interception and water use characteristics (Loomis and Williams, 1969), these architectural traits may be important considerations in the development of cultivars adapted to specific light environments (i.e., northern vs. southern orchard sites).

Pecan tree height and trunk cross sectional area increased as latitude decreases and as elevation increases. In a previous study by Toliver and Zeringue (1983) of 6-year-old seedlings from nuts collected from several pecan stands in central Louisiana, only random variation was observed in tree height among stands. Our data show that variation exists in height. Adams (1976) observed that in certain pecan provenances (from Oklahoma, Louisiana, and northeastern Texas) 21% of the variation in first-year seedling growth was due to seed size, with trees from large nuts being larger. However, this relationship diminished as trees aged. In the present study, only 5% of the variation in tree height, at seven years in the field, was associated with seed weight (data not shown), thus, suggesting that, in the long term, there may be little gained in tree height by selecting heavy seeded genotypes.

Morphological characteristics of pecan conformed to the para-

Table 5. Heritability and standard error estimates of vegetative traits of pecan based on 19 provenances growing at a single location in single tree plots. Estimates were determined by the restricted maximum likelihood methods.

Trait	Family		Single tree	
	h_f^2	δh_f^2	h_t^2	δh_t^2
Budbreak	0.67	0.12	0.68	0.04
Leaf fall	0.39	0.08	0.24	0.03
Tree height	0.58	0.10	0.49	0.03
Trunk area	0.59	0.11	0.52	0.03
Zinc deficiency	0.14	0.06	0.07	0.02
Aphid resistance	0.37	0.08	0.24	0.03
Red coloration	0.48	0.09	0.35	0.03
Cold damage	0.68	0.12	0.72	0.04
Branch angle	0.21	0.07	0.12	0.02
Leaflet droop angle	0.49	0.09	0.38	0.03
Leaflet tilt angle	0.49	0.10	0.39	0.03

digm typical of most North American tree species in that southern sources generally grew faster, retained leaves later in the fall and were less resistant to extreme winter cold (Wright, 1976). However, deviations from this paradigm also occurred. For example, southern sources leafed out earlier in the spring than did northern sources and sources from dry regions grew taller faster than those from wetter regions. These N-S trends are reversed in many species, such as Douglas-fir [*Pseudotsuga taxifolia* (Poir.) Britt.] and black walnut [*Juglans nigra* (L.)] (Wright, 1976). These anomalies indicate that certain natural variation patterns in pecan may markedly differ from that of most North American tree species (Wright, 1976). This possibly indicates that either the evolutionary forces associated with the interaction of pecan with its environment is different than is typical for most trees or that pecan germplasm has migrated either by man or by animals within the putative natural range.

The low heritabilities of limb angle and zinc deficiency indicates that breeding gains for these traits may be slow whereas gain for height, diameter, red coloration, leaflet angles, and aphid resistance would likely be rapid. These estimates compare favorably with individual estimates (via regression) for pecan nut characteristics where estimates were: nut weight (0.35), buoyancy (0.18), volume (0.35), density (0.03), kernel weight (0.38), and percentage kernel (0.32) (Thompson and Baker, 1993).

In summary, these data indicate considerable genetic variation within the species, provide a rough estimate of the total range of genetic variation for important vegetative traits, identify populations of pecan with the capacity to produce above average individuals in regards to the traits evaluated, and provide heritability estimates for these traits. These data provide clues as to the nature of genetic improvement that is likely to be derived from intensive breeding and suggests parental materials for specific traits. Cluster analysis indicates that the natural range of pecan can be subdivided into at least two subdivisions with populations in Texas and Mexico being markedly different than populations north of Texas.

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