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GENOTYPIC VARIATION AND SELECTION IN
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GENOTYPIC VARIATION AND SELECTION

IN *JUGLANS NIGRA* L.

by

Calvin Frederick Bey

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INTRODUCTION

Black walnut (<u>Juglans</u> <u>nigra</u> L.) is an important forest tree species in eastern and central United States. It is found naturally from Minnesota to Texas and from Kansas to the East Coast. Over this range, the annual rainfall varies from less than 25 to over 70 inches; the mean annual temperature varies from 45 to 67 degrees; and the frost-free season varies from 140 to 280 days (United States Department of Agriculture 1965a).

Black walnut rarely occurs in pure stands. It is generally scattered among yellow-poplar, white ash, black cherry, basswood, beech, sugar maple, oaks and hickories. It grows best on deep, well-drained, nearly neutral soils which are usually moist and fertile (Auten 1945). Most walnut plantations have had low survival and/or slow growth. Off-site planting and the lack of weed control for the first few years probably accounts for most of the failures.

Supplies of high-quality black walnut logs are dwindling. The annual cut of high-quality material exceeds the annual increase in quality material. At the same time, demands for walnut have been increasing. Consumption of veneer logs rose from 8.5 million board feet in 1955 to 38.5 million in 1963. During the same period exports increased from 1.2 million to 15.0 million. The shortage of high-quality walnut occurs throughout the Midwest region, which is the major production area for high-quality walnut logs (Quigley and Lindmark 1966).

Since Colonial days in America, black walnut wood has been a favorite for furniture, paneling, gunstocks, and art carvings. It is a strong, hard wood and yet it is easy to work. Limited tests have indicated that wood from fast-grown trees is equal or superior in planing, shaping, and turning qualities than wood from slow-grown trees. In addition, the fast-grown material had a higher specific gravity and was tougher (Englerth 1966).

From the standpoint of veneer and lumber production, the most valuable black walnut tree has a round and straight stem, no side branches on the lower portion of the stem, and a uniform and rapid growth rate. Past experience has demonstrated that in order to achieve this in plantations, we will have to use intensive cultural practices, which include weed control and corrective pruning as a minimum. Intensive culture during the establishment phase implies higher costs, which must be carried for the entire rotation. The magnitude of the response to any cultural treatment will be limited by the genetic constitution of the trees in the population. To partially offset the added cultural expenses, it will be important to plant trees that have the inherent capacity for rapid growth, straight boles, and insect and disease resistance. Past work with agronomic crops and other forest trees has demonstrated the high value of selection and hybridization efforts. To obtain maximum production and quality, we must also examine the possibilities of improving the tree through genetic manipulation.

The choice of seed is an important factor affecting the growth and quality of forest plantations. Large differences in growth, hardiness, and form often are evident when seed from widely divergent sources are grown under uniform environmental conditions (Wright 1962). It is not surprising that we get big differences in response when the sources concerned have developed under different climatic, edaphic, and biotic conditions. Natural selection, in response to forces of the climate, soil and biotic community, are responsible for maintaining or rejecting the variants in the population.

Seed source studies (also called provenance studies) are aimed at defining the genetic and environmental components of phenotypic variability between trees from different geographic origins. For black walnut, we need to know the type of variation (ecotypic or clinal) and have estimates of variation within stands, and between stands. The estimates of variation will help us in selecting superior genotypes more efficiently. For example, if within stand variance is 4X and between stand variance is 5X, it might be more efficient to select from within stands only. This assumes genotype by environment interaction (performance) is acceptable from either situation. If, however, within stand variance is X and between stand variance is 5X, it is likely that it would be more efficient to select between stands. Knowing the type and pattern of variation would also be useful in a hybridization program. If the variation pattern is ecotypic, we may want to select and cross individuals from diverse ecotypes. If the pattern is clinal, we may want to select and cross from the most diverse parts (genetically) of the range. Hybrids from parents of diverse origin may result in hybrid vigor for many characters (Clausen and Hiesey 1958).

PART I. GEOGRAPHIC VARIATION IN BLACK WALNUT

REVIEW OF LITERATURE

The earliest known work of natural variation in black walnut is described by Emerson (1906). Seed was collected in 18 states and planted in a nursery in Nebraska. Observations during the first eight years showed that trees of southern provenance held their leaves later in the fall and suffered more cold injury as contrasted to those from northern provenances. Maturity, as measured by leaf fall and terminal bud development, was closely related to the degree of winter injury. By September 19, 1902, the terminal buds on the South Dakota and Nebraska trees were well developed and the wood was thick and firm, while in the case of the twigs from South Carolina and North Carolina trees, the terminal buds were immature and the layer of wood near the top scarcely differentiated from the pith. Although some trees from the northern sources were able to escape winter injury, a comparatively light freeze late in the spring of 1903 killed the new growth of the northern trees just as completely as it did that of the southern ones.

No data on survival and relative growth are available from Emerson's report (1906). It should be pointed out that trees from as far south as Georgia, Alabama, and South Carolina were able to survive the much colder climate of Nebraska for at least eight years. Although no height data are provided, in the photographs depicting the various stages of leaf fall, the southern trees appear to be at least as tall as the northern trees.

Wright (1954) reported on a walnut seed source study conducted at Purdue University. Seed was collected from 28 parent trees in 18 states throughout the range of the species and planted in north-central Indiana.

Data were collected on nut size, survival and height growth. There were no correlations between origin and nut size, origin and survival, height and degree of germination before planting, or between seed weight and height growth. The trees were grouped by three main regions--Northwest, Central and South. Significant differences in height growth were found between and within regions. The trees from the South held their leaves longer than trees from the North. Wright (1954) suggests that three races of walnut might exist on the basis of the length of the frost-free season. Survival was 28 percent after three years and the study was terminated.

Except for the higher elevations in the Appalachian Mountains, the pattern for the normal length of the frost-free season corresponds roughly to degrees of latitude. Although large bodies of water, elevation differences, and local air drainage patterns are likely to cause minor changes in the overall pattern, the major variation pattern for the normal length of the frost-free season is continuous. It would be reasonable to expect some characters in black walnut to also exhibit a continuous variation pattern.

Selection of walnut trees with the inherent capacity to produce high-quality nuts and high nut yield has received attention by the Tennessee Valley Authority (Zarger 1946), State Agriculture Experiment Stations (Atwood and Mac Daniels 1946), and many members of the Northern Nut Growers Association (Weber 1964). More than 500 black walnut selections have been tested by the Tennessee Valley Authority in eastern Tennessee, northern Alabama, and in the mountainous region of North Carolina and southern Virginia. Out of the 15 selections classified as "best", 13 were from areas north of the test planting area. Whereas, of the 15 classified as "poor" selections, only 7 were from areas north of the test planting area. It appears that there may be regional differences in nut quality characteristics (Zarger 1946).

Black walnut trees flower in the spring. They are classified as monoecious and dichogamous. The fruit reaches full size in August and falls to the ground soon after the leaves fall, normally in October. The seed requires a cold and moist treatment (stratification) of at least 90 days before it will germinate.

Most walnut trees begin bearing seed about 10 years after planting. With intensive cultural treatments and rapid early growth, the seed bearing age is expected to be reduced by several years. Grafted walnut trees normally flower within 4 years after field planting. A good seed crop can be expected only every other year. Sometimes a tree will bear abundantly two years in a row and then return to the alternate year cycle (Taft 1966). Seed production depends on the size of the crown. Mature, open-grown trees will sometimes produce 20 bushels of seed, while many forest-grown trees with relatively small crowns may bear little or no seed for several consecutive years.

All members of the genus _Juglans_ have a diploid chromosome number of 32 (Woodworth 1930). _Juglans nigra_ has been crossed with a number of other species in the genus (Howard 1945, Reed 1937). Some progeny from _Juglans regia_ x _Juglans nigra_ have exhibited hybrid vigor (Wellington 1931, Schuster 1937).

Black walnut can be propagated vegetatively through grafting or budding (Chase 1947a, Davis 1963). This procedure is costly and is not used in mass production operations. As elite material becomes available, the costs may be justified. Black walnut cuttings have been essentially impossible to root.

MATERIAL AND METHOD

Seed Acquisition

Black walnut seed was collected from 97 stands located throughout 21 states in Eastern and Central United States (Figure 1 and Table 1). The cooperators who assisted in seed collection included U. S. Forest Service Researchers, U. S. Forest Service District Rangers, State Foresters, and State Service Foresters. The author personally collected some of the seed from Iowa, Kansas, and Missouri. The response from cooperators was generally good.

An attempt was made to get seed from 100 stands throughout the range. Requests for seed were sent to approximately 170 cooperators located throughout the range of the species. An attempt was made to get an equal number of seed from each stand and an equal number of stands in each part of the range. In reality, the author had to accept seed from where our cooperators could find it.

Seed was collected from a wide range of latitudes and longitudes. Latitude ranged from 30° 28' N in southeastern Texas to 44° 21' N in southern Minnesota. Longitude ranged from 76° 07' W in northeastern Pennsylvania to 96° 23' W in northwestern Iowa. Elevation varied from 27 meters in Maryland to 884 meters in North Carolina.

Each cooperator was requested to collect seed from anywhere within a three or four county area. It was not always possible for the cooperator to find seed in the area specified by the author. In some cases, walnut trees did not occur in that particular area and in other cases the trees did not have seed. Most cooperators collected seed from areas close to

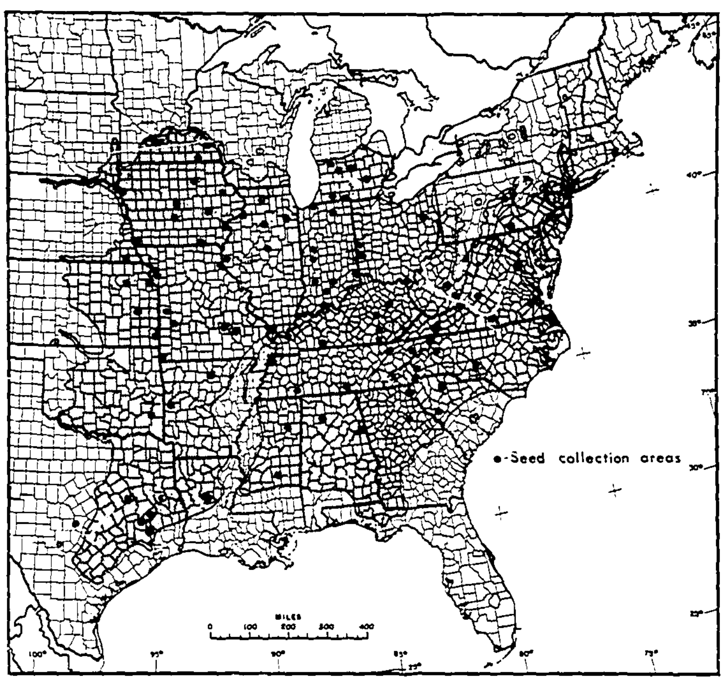

Figure 1. Black walnut seed was collected from 97 stands throughout Eastern and Central United States.

Table 1. Black walnut seed was collected from 97 stands located throughout Eastern and Central United States

Stand number	State	County	North latitude	West longitude	Elevation
			Degrees and Minutes		Meters
1001	Alabama	Cleburne	33 40	85 32	366
1002	Alabama	Winston	34 10	87 15	183
1101	Arkansas	Stone	35 50	92 20	366
1102	Arkansas	Scott	34 59	93 57	584
1501	Georgia	Greene-Clarke	33 45	83 17	198
1601	Illinois	Union	37 26	89 16	165
1602	Illinois	Rock Island	41 33	90 25	183
1603	Illinois	Putnam	41 10	89 10	214
1604	Illinois	McLean	40 20	89 10	214
1605	Illinois	Will	41 23	88 08	186
1606	Illinois	Adams	40 11	91 21	183
1607	Illinois	Ogle	41 55	89 16	241
1701	Indiana	Orange	38 39	86 27	195
1702	Indiana	Putnam	39 50	86 57	223
1703	Indiana	Kosciusko	41 25	85 46	267
1704	Indiana	Jackson	39 00	86 06	238
1705	Indiana	Montgomery	40 10	86 55	183
1706	Indiana	LaPorte	41 40	86 45	244
1707	Indiana	Dearborn	39 16	84 58	290
1708	Indiana	Perry	38 10	86 37	236
1709	Indiana	Greene	39 03	86 55	149
1801	Iowa	Story	42 07	93 37	290
1802	Iowa	Iowa	41 47	91 52	214
1803	Iowa	Delaware	42 20	91 14	274
1804	Iowa	Davis	40 40	92 30	290
1805	Iowa	Polk	41 32	93 40	239
1806	Iowa	Story	42 01	93 38	290
1807	Iowa	Butler	42 50	92 47	290
1808	Iowa	Louisa	41 15	91 10	183
1809	Iowa	Woodbury	42 30	96 23	336
1810	Iowa	Fremont	40 46	95 40	336
1901	Kansas	Pottawatomie	39 08	96 05	320
1902	Kansas	Anderson	38 18	95 12	297

Table 1. (Continued)

Stand number	State	County	North latitude	West longitude	Elevation
			Degrees and Minutes		Meters
1903	Kansas	Leavenworth	39 07	94 55	274
1904	Kansas	Crawford	37 20	94 40	268
2001	Kentucky	Logan	36 53	86 48	159
2002	Kentucky	Menifee	37 58	83 31	305
2003	Kentucky	Whitley	36 42	84 07	518
2004	Kentucky	Laurel	36 59	84 18	351
2005	Kentucky	Madison	37 34	84 16	336
2101	Louisiana	Grant	31 32	92 26	38
2201	Maryland	Charles	38 32	77 13	27
2401	Michigan	Clinton	42 47	84 30	274
2402	Michigan	Branch	41 50	85 00	290
2403	Michigan	St. Joseph	41 55	85 45	256
2404	Michigan	Ionia	42 46	85 15	229
2405	Michigan	Livingston-Washtenaw	42 30	83 50	259
2406	Michigan	Kent	43 08	85 40	244
2501	Minnesota	Mower-Fillmore	43 35	92 15	396
2502	Minnesota	Winona	44 05	91 50	210
2503	Minnesota	Brown	44 21	94 31	305
2601	Mississippi	Scott-Smith	32 15	89 28	137
2602	Mississippi	Chickasaw	34 01	88 55	122
2701	Missouri	Buchanan	39 47	94 50	314
2702	Missouri	Buchanan	39 35	94 49	268
2703	Missouri	Cedar	37 52	93 56	282
2704	Missouri	Dent	37 38	91 30	357
2705	Missouri	Marion	39 43	91 25	201
2706	Missouri	Reynolds	37 25	91 00	242
2707	Missouri	McDonald	36 37	94 26	274
2708	Missouri	Bates	38 16	94 08	244
2801	Nebraska	Pawnee	40 09	96 04	358
3101	North Carolina	Caldwell	36 00	81 41	458
3102	North Carolina	Graham	35 22	83 43	884

Table 1. (Continued)

Stand number	State	County	North latitude	West longitude	Elevation
3103	North Carolina	Transylvania	35 17	82 45	762
3104	North Carolina	Montgomery	35 26	79 53	214
3105	North Carolina	Buncombe	35 30	82 38	671
3201	Ohio	Preble	39 45	84 33	281
3203	Ohio	Darke	40 06	84 43	305
3203	Ohio	Lawrence	38 37	82 35	183
3204	Ohio	Stark	40 38	81 21	336
3301	Oklahoma	Push	34 32	95 05	152
3501	Pennsylvania	Wyoming	41 32	76 07	396
3502	Pennsylvania	Union	40 57	77 10	195
3503	Pennsylvania	Adams	40 01	77 08	195
3601	South Carolina	Edgefield	33 51	82 07	156
3602	South Carolina	Union	34 40	81 40	183
3603	South Carolina	Oconee	34 51	83 03	549
3801	Tennessee	Greene	36 10	82 52	518
3802	Tennessee	Franklin	35 12	85 55	518
3803	Tennessee	Union	36 20	83 44	389
3804	Tennessee	Johnson	36 22	82 00	622
3805	Tennessee	Obion	36 22	89 24	198
3806	Tennessee	Hardin	35 12	88 19	146
3901	Texas	Freestone	31 34	96 00	110
3902	Texas	Nacogdoches	31 33	94 36	94
3903	Texas	Trinity	31 05	94 56	79
3904	Texas	Walker	30 52	95 23	107
3905	Texas	San Jacinto	30 28	95 12	76
4101	Virginia	Rockbridge-Amhurst	37 45	79 28	305
4102	Virginia	Craig	37 33	80 08	442
4103	Virginia	Halifax	36 51	78 44	140
4104	Virginia	Surry	37 05	76 52	37
4105	Virginia	Smyth	36 50	81 31	656
4201	West Virginia	Webster	38 17	81 28	747
4202	West Virginia	Greenbrier	37 56	80 13	595
4203	West Virginia	Tucker	39 04	79 42	515

the designated areas. In 1965 the nut crop was low in the northern portion of the range. In many cases, the author found it difficult to locate stands of walnut with 5 to 10 fruitful walnut trees. Cooperators collected and sent in seed from one to twelve trees per stand. Six was the average number of parent trees per stand from which seed was collected. In order to include a sampling point in some areas, open-grown trees were used as parent-trees. Open-grown trees are usually much heavier producers of seed than are the forest-grown trees. The author assumes that the open-grown trees are as representative of the genotypes of the areas as are the forest-grown trees. Open-grown trees are generally open-grown simply because the other trees (probably other species) growing around them have been removed.

Each cooperator was requested to collect seed from trees that had a form that was typical for the area. In this case "form" refers to stem straightness. However, in many cases trees that were above- and below-average in "form" were used. An attempt was made to collect from ten dominant and/or codominant trees located at least 50 feet apart but in an area not larger than ten acres. The 50-foot minimum was used to get a representative sample of the genotypes of the area. If all the seed was collected from trees in a very small area, the within stand variance would likely be reduced because of inbreeding. In some cases, cooperators had to go beyond the ten-acre limit to find enough trees with seed.

All seed collected came from natural stands. In almost every case, the trees were in mixed stands. Walnut rarely occurs in pure stands naturally.

Although seed was requested from ten trees in each stand, it was not always possible to meet this requirement. The author felt that the physical limitation in this study would be progeny from 500 parent trees. Progeny from a parent tree is hereafter called a "family". It was assumed that within stand variance would be small compared with between stand variance, and consequently regional variation pattern could be defined more accurately by using a large number of stands and fewer trees per stand. Wright (1963) and Ruby (1967) have shown that within stand variation is small compared with between stand variation for scotch pine. Wells (1964) has also shown this to be true for ponderosa pine.

Seed Handling and Nursery Treatment

The seed arrived from September 1965 through January 1966. Most of the seed arrived in October and November 1965.

Most of the seed that arrived had not been cleaned (hulls removed). Seed with hulls was placed in a storage building and dampened twice a week until the hulls were soft and mushy. The hulls were removed in a corn husker and then placed on a screen and washed with running water. After the seed was washed, seeds which were grayish-brown in color or which had worm holes or were cracked or had broken shells were discarded. Cracking tests revealed that grayish-brown seed were almost always empty.

Twenty-five seeds were then randomly picked. They were weighed to the nearest gram. The volume was measured to the nearest cubic centimeter by immersion in water. Only families which had seed with a specific gravity of 1.00 or greater were used in the experiment. After cleaning and weighing the nuts were put in small plastic bags. A small amount of water (25-50 ml) was put in each bag to insure against drying out. The bags were closed and tied with wire and a numbered label was attached. A plastic label was also put in the bag. The bags were placed on a concrete floor in the storage shed. When the majority of the nuts had been cleaned and weighed (November 15, 1965), they were moved to the seedling storage cave, where there was a constant temperature of 2° C. and a high relative humidity. The nuts were checked monthly to be sure they remained moist.

On May 18, 1966 all of the nuts were taken out of the cold storage cave and placed on the ground where they were exposed to the warm sun. After one day, many nuts had germinated. Planting was started on May 19 and completed on May 21. Twelve hundred pounds of 8-32-16 fertilizer per acre was added before planting. The fertilizer was broadcast on the surface and roto-tilled in the top 20 cm of the soil. After the fertilizer was roto-tilled in, one pound per acre (active ingredients) of Treflon was sprayed on the surface. The Treflon was roto-tilled in to an 8 cm depth. Two inches of rain fell one day after planting. This insured that the nuts were well sealed in moist soil. Ground squirrels were observed digging up and eating some of the nuts. The amount of loss varied from none in some areas to heavy in others.

Experimental Design

A randomized complete block design was used in the nursery. There were six blocks. Each block contained 480 plots (families) representing 78 stands. Low germination in some sources and rodent pilferage in others reduced the total number of plots to 1840. Figure 2 shows a general view

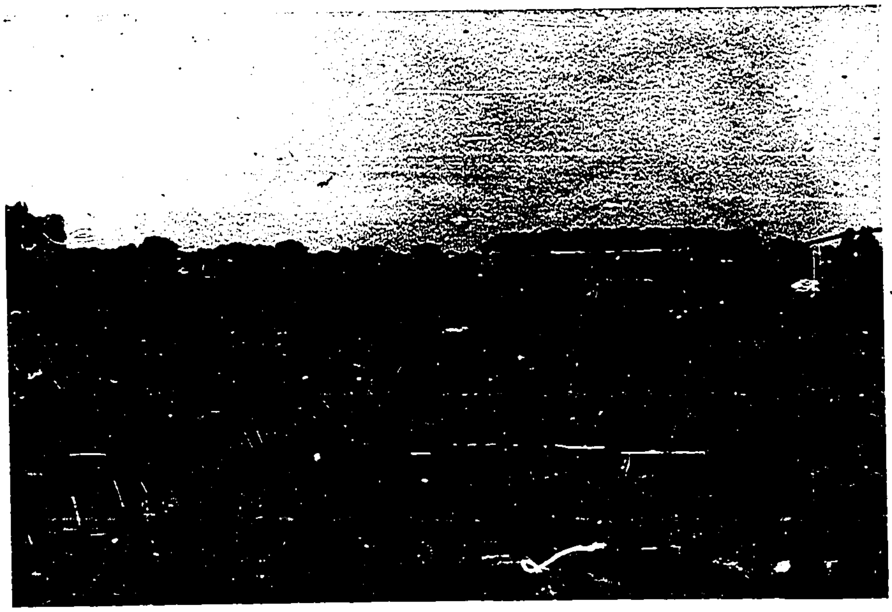

Figure 2. General view of black walnut seedlings in the nursery.

of the seedlings in the nursery. The number of families per stand varied from two to twelve with an average of six. In each plot four seed were planted. The seed were spaced one foot apart in the row. There was also one foot between rows (plots or families).

This experimental design was used to: (1) determine whether genotypic variability in black walnut is ecotypic or clinal and to define the limits of ecotypes where they existed, (2) obtain estimates of genotypic variance within stands and between stands, and (3) obtain estimates of correlation between characters.

Data Collected

Seed size

Data was collected on seed size immediately after the seed was cleaned. Twenty-five seed from each parent tree were randomly selected. The 25-seed lot was weighed to the nearest gram and their volume determined by submersion in water.

Four hundred and fifty-six families from 69 stands were used for making the seed-weight comparisons. The sources and families had to meet the following criteria to be used in the analysis: (1) The specific gravity for any 25-seed sample must be 1.00 or greater. Seed with specific gravity of less than 1.00 are likely to be only partially filled and therefore would represent a biased sample. (2) There must be at least four families per source with a specific gravity of 1.00 or more for the source to be used. The four-trees per source criterion was arbitrarily chosen.

Data were collected on the seedlings in the nursery during and at the end of the first growing season. The following variables were measured:

1. Leaf color
2. Insect damage
3. Leaf angle
4. Total height in August
5. Leaf length in August
6. Date of leaf drop
7. Total height at end of growing season
8. Diameter 2.5 cm above root color at end of growing season
9. Number of trees with multiple stems

<u>Leaf color</u>

Leaf color of the newly developing leaves was recorded on July 28-30, 1966. The evaluation was based only on leaves less than 15 centimeters long. The following rating and coding scheme which was used was subjective and based on the amount of red pigment visible to the eye:

Code	Color of new leaves
1	All new leaves red
2	New leaves mostly red, but a small amount of green visible
3	New leaves pinkish (about half-way be tween all green and all red)
4	New leaves mostly green, but still a hint of pink or red
5	All new leaves green

The evaluation was based on the plot average. The author and Ross Writer (Forestry Aid) spent about one hour practicing the subjective evaluation before recording any data. Each plot was scored independently by both men. If a disagreement occurred, the plot was discussed in terms of previous plot ratings. Representative sample leaves were selected and photographed (Figure 3).

The Munsell system of leaf color notation was tried. It proved to be too time consuming to be used for this experiment. The variation in color of mature leaves was so minor that an evaluation was not attempted.

Insect damage

Insect damage was observed in June and July. At no time did the infestation reach epidemic proportions. In late June, I observed a number of seedlings which had terminal buds missing. A closer examination revealed that associated with the missing bud was an insect rolled in one of the young leaves near the terminal bud. The insect was identified as the fruit tree leaf roller, *Archips argyrospila* (Wlkr). It appeared that this insect was responsible for eating the terminal bud and adjacent new leaves. The result of this damage was multiple stemmed seedlings. Other insects, which were observed chewing on the walnut leaves, were identified as the white-marked tussock moth, *Hemerocampa leucostigma* (A. and S.) velvet bean caterpillar, *Anticarsia gemmatalis*, and the walnut caterpillar, *Datana integerrima* (G. and R.). Insect damage was assessed on August 9, 1966, by counting the total number of leaves per plot which had portions missing as a result of insect chewing. The average number of chewed leaves per plant was recorded.

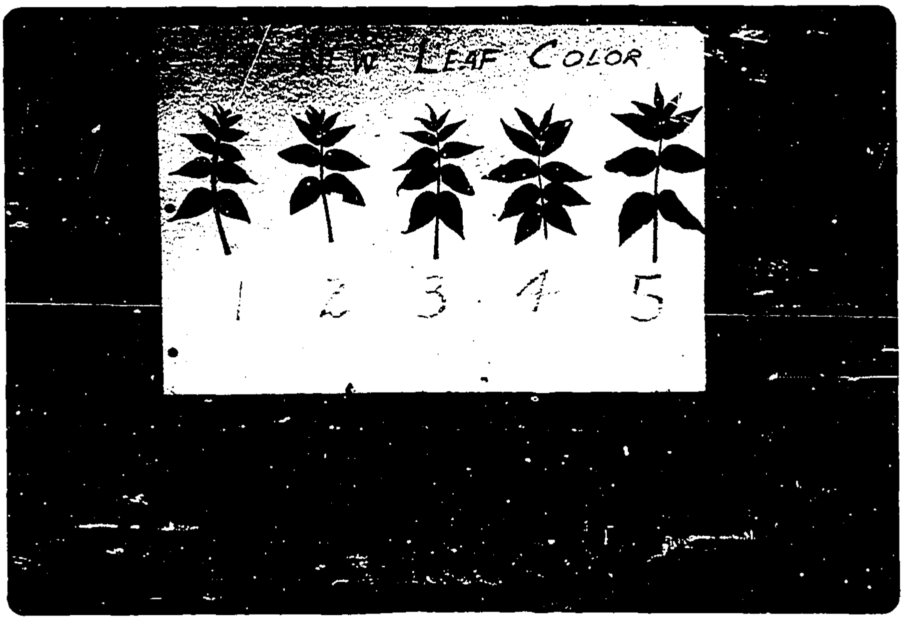

Figure 3. The amount of red pigment visible to the eye in the newly developing leaves was estimated.

Leaf angle

Leaf angle of the mature leaves near the top of the plant was estimated on August 10, 1966. The upper mature leaves of an individual plant were considered to be the most uniform for leaf angle measurements. Variation in leaf angle between individual leaves was obviously present but not measured. After actually practice-measuring leaf angle on a series of seedlings, the leaf angle was estimated for each plot and recorded according to the following code:

Leaf angle away from the vertical measured in degrees	Code
Less than 30	1
30-40	2
41-50	3
51-60	4
Greater than 60	5

This was a subjective evaluation and a procedure similar to leaf color estimation procedure was followed. The estimations were made by the author and Ross Writer. If a disagreement as to a particular rating occurred, the plot was discussed and compared with previously rated plots until the disagreement was resolved. It was quite easy to pick out the five leaf angle classes. An occasional disagreement between classes 3 and 4 occurred.

Total height in August

Total height of the tallest seedling in each plot was measured on August 11-12, 1966. The tallest seedling was considered to be the most mature and most representative for use in the height-leaf length ratio computation.

Leaf length

The length of the longest leaf on the tallest seedling was also measured on August 11-12, 1966. The longest leaf was selected to standardize the measurement procedure. In most cases, an average of the two or three longest leaves would differ very little from the longest leaf measurement.

Date of leaf drop

Date of leaf drop was recorded for each plot. The date of leaf drop was recorded when all of the trees in a plot except one had lost at least most of their leaves. "Most" of the leaves means all of the leaves on each tree except one. In plots where there was only one seedling, that one seedling must have lost at least all of its leaves except one before leaf drop was recorded. In two-, three-, and four-tree plots all trees except one must have lost at least all of its leaves except one.

Total height

Total height at the end of the growing season was measured on the tallest seedling in each plot. In some plots seeds germinated in July and August and had grown only a few centimeters. Those plots with late-germinating seedlings would have contained a bias if plot averages were used.

Stem diameter

Stem diameter at the end of the growing season of the tallest seedling in each plot was measured. The diameter was measured 2.5 centimeters above the ground line.

<u>Number of trees with multiple stems</u>

The number of trees with multiple stems in each plot were counted at the end of the growing season. Since the total number of seedlings per plot varied from one to four, a percentage of the trees with multiple stems was recorded. This figure was transformed to arcsin per cent before analysis.

Analysis

<u>Developing the models</u>

The significance of the data for each character was evaluated by analysis of variance (AOV), using blocks 1-3. Tukey's w-procedure for making multiple comparisons was used (Steel and Torrie 1960).

The data for stem height and stem diameter were adjusted for differences in size of the seed. Chase (1947b) has shown that for black walnut, stem height and diameter are influenced by the kernel weight and total seed weight. Large seed produce the large seedlings. Seed weight is generally indicative of kernel weight. The kernel weight makes up about 20 percent of the seed weight and is a slightly better indicator of seedling size than is seed weight. To use kernel weight as an indicator of seedling size requires destruction of the seed. Because of the scarcity of seed in some families and the amount of work required to determine kernel weight, seed weight was used as the covariate variable. The height and diameter values were adjusted for differences in the seed weight, using standard covariance analysis procedure (Steel and Torrie 1960). The adjusted values were used in the AOV.

Tukey's w-procedure requires the determination of only a single critical value for judging the significance of all differences for each character. Fewer differences are declared significant by Tukey's procedure than by Duncan's multiple range test. Since this is preliminary work and trends are being sought for, a 10 percent error rate was used. Hartley (1955) suggests that the error rate be relaxed to 10 percent or even higher. Tukey's w-procedure consists of computing

$$w = q_{.10}\ (p_1 n_2) s_{\bar{X}}$$

where $q_{.10}$ is obtained from a table for $\alpha = .10$, p is the number of treatments and n_2 equals error degrees of freedom. No tables for comparison beyond 20 means of the upper 10 percent points of the studentized range test were available. A graphic extension of the curve beyond 20 means indicated that the $q_{.10}$ (78, 154) value should be approximately 5.5. The standard error of a treatment mean ($s_{\bar{X}}$) was computed as

$$s_{\bar{X}} = \sqrt{(\text{error mean square})/r}$$

where r is the number of observations in each treatment.

A critical value was determined for each of the characters measured. Where differences between sources occurred, an attempt was made to relate the differences of latitude, longitude, altitude or a combination of these variables. Using data from blocks 1-3 models of the pattern of variation were suggested. Continuous and discontinuous patterns were explored. Tests of the significance of linear regressions for blocks 1-3 were run for the purpose of developing the models. Only the model which seemed to best explain the pattern of variation for each character was tested.

Testing the models

After a model for the variation pattern for each character was established, it was tested with data from sources in blocks 4-6. Where the data suggested that variation was ecotypic, the ecotypic boundaries were delineated and an analysis of variance test was run to determine if differences between ecotypes existed.

Where the data suggested that the variation pattern was continuous, blocks 4-6 were used to test the significance of the regression model. If the regression for blocks 4-6 was significant, the data for all blocks was combined for the best estimate of the slope. The variance of the sample regression coefficient (S_b^2) was computed for each regression.

RESULTS

The Pattern of Variation

Seed size

There were no significant differences at .05 level in average seed weight between sources (Table 2). The lack of significance was not surprising. The observations made while cleaning the seed were that there seemed to be more variation within than between sources.

The average seed weight for 456 families from 69 sources was 22 grams per seed. The average weight per source varied from 12 to 30 grams per seed. Families varied from 5 to 40 grams per seed (Figure 4). A range of 10 grams or more (average seed weight) between families within the same source occurred in 59 percent of the sources. It has been the author's observations that seed size within a family is very uniform. Also, a tree that produces large nuts one year is likely to do so every year.

Leaf color

Seven sources differed significantly in leaf color from many of the remaining 71 sources. They all had a leaf color rating of 3.00 or less. This means that new leaves tended to be red. All of the seven sources occurred in the southeastern part of the range. Altitude for the seven sources varied from 146 to 884 meters. It appeared that a southeastern ecotype existed, and an ecotype boundary was delineated. All sources from North Carolina, South Carolina, Georgia, Alabama, Mississippi, and Tennessee (except one western source) were grouped as one ecotype and

Table 2. Mean squares from analysis of variance and critical values for nine characters

Character	Mean square: Block - B 2 d.f.	Mean square: Source - S 77 d.f.	Mean square: B x S 154 d.f.	Critical value[a]
Leaf color	2.08	1.36**	.29	.84
Insect damage	23.75	6.11**	2.93	2.66
Leaf angle	.50	.58**	.31	.87
Height-leaf length ratio	12,087.38	2,354.41**	433.94	32.40
Leaf drop	125.53	19.36**	3.47	2.90
Multiple stem frequency	1,046.00	478.45**	166.06	20.02
Adjusted stem diameter	36.39	9.20**	2.81	2.61
Adjusted stem height	5,910.39	545.15**	108.46	16.20
Seed weight	-	36.93[NS]	28.22[b]	-

[a]Critical value = $q_{.10}(p_1 n_2) s_{\bar{x}}$.

[b]Within source mean square used as error term for testing between sources.

**Significant at .01 level.

[NS]No significant differences at .05 level.

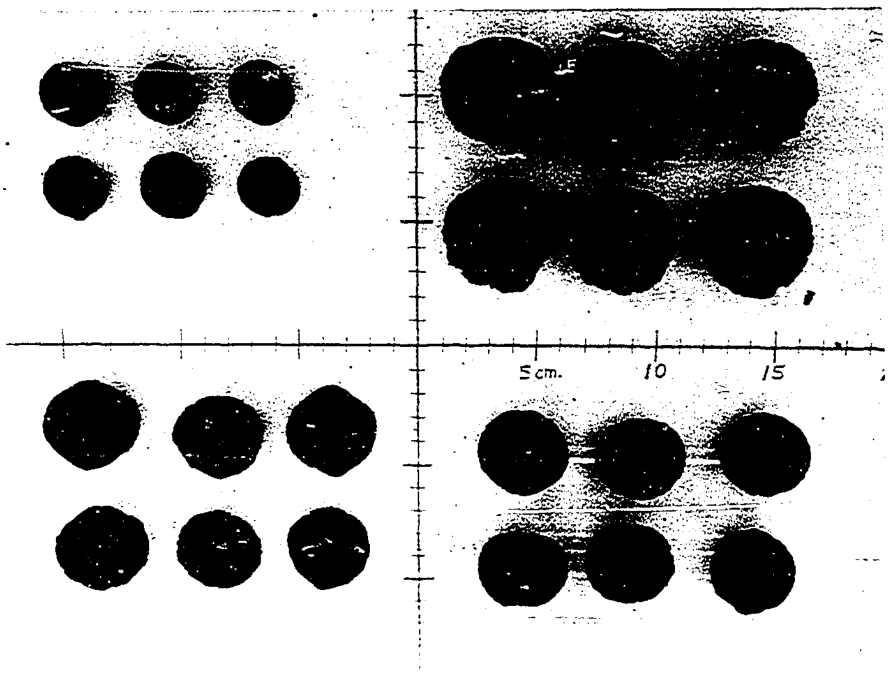

Figure 4. Average seed size for 456 families varied from 5 to 40 grams per seed.

tested against all the other sources (the second ecotype).

Using the data from blocks 4-6, the AOV test revealed that the southeast ecotype was significantly different from the rest of the population (Table 3 and Figure 5).

Insect damage

Although the F test showed insect damage was significantly different between sources, Tukey's multiple range test showed that only a few sources were significantly different from any other sources. Over 90 percent of the sources were not different from any other sources. For the few sources that were different, there was no pattern over the range of the species. Of the four very resistant (least chewed) sources, two were from the northern and two were from the southern portion of the walnut natural range. The three most susceptible sources were from widely different geographic areas--Iowa, Michigan, and Tennessee.

On the basis of these data, it appears that the chewing insects have little or no preference for walnut leaves from particular sources. For the most part, chewing occurred at random.

Leaf angle

The multiple range test revealed that only five sources were significantly different in leaf angle from any other sources. No geographic variation pattern was discernible. The two lowest (narrowest branch angle) sources occurred in Iowa and Nebraska, while the three highest (wide branch angle) occurred in Indiana, Illinois and Texas.

On the basis of this data, it appears that there is no regional variation pattern for leaf angle. No model for the pattern of variation in leaf angle is suggested.

Table 3. Analysis of variance table for leaf color by ecotypes

Source of variation	Degrees of freedom	Sums of squares	Mean square
Block - B	2	1.64	
Ecotype - E	1	33.06	33.06*
B X E (experimental error)	2	.93	.46
Total	5	35.63	

*Significant at .05 level.

Height-leaf length ratio

There were a large number of differences between sources for the height-leaf length ratio. The values were plotted over altitude, longitude, latitude, and in a three dimensional graph using longitude and latitude as the x and y coordinates. There appeared to be a linear north-south trend. A linear regression analysis of the data in blocks 1-3 and a test for significance revealed that the regression was significant at the .01 level (Table 4).

Using the data from blocks 4-6, a linear regression was run and tested for significance. It was significant at the .01 level. The data for blocks 1-6 were pooled for a better overall estimate of the slope (Figure 6). The regression equation for the combined data was

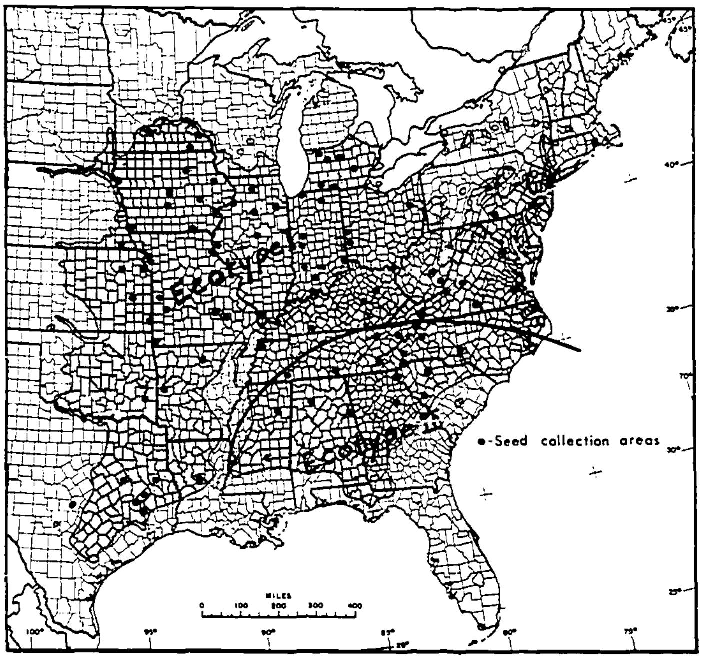

Figure 5. Two ecotypes for leaf color have been delineated.

$y = 238.32 - 3.64x$. The variance of the sample regression coefficient was .12.

Leaf drop

There were a large number of differences between sources for date of leaf drop. The values were plotted on a graph and there appeared to be a linear north-south trend. Blocks 1-3 were analyzed using linear regression. A test of the data revealed that the regression equation was significant at the .01 level (Table 4).

Using data from blocks 4-6, a regression was run using the linear model developed from blocks 1-3. The linear regression was significant at the .01 level. Data from blocks 1-6 were pooled for a better overall estimate of the slope (Figure 7). The regression equation for the combined data was $y = 31.66 - .38x$. The variance of the sample regression coefficient was .004.

Multiple stems

There were a large number of differences between sources for frequency of multiple stems. The values were plotted on a graph and there appeared to be a linear north-south trend. Blocks 1-3 were analyzed using linear regression. The regression was significant at the .01 level (Table 4).

Using data from blocks 4-6, a regression was run using the linear model developed from blocks 1-3. The regression was significant at the .01 level. Data from blocks 1-6 were pooled for a better overall estimate of the slope (Figure 8). The regression equation for the combined

Table 4. Mean squares from analysis of variance tables for testing significance of linear regression for height-leaf length ratio, leaf drop, multiple stem frequency, adjusted stem diameter and adjusted stem height over latitude of seed source for blocks 1-3 and 4-6

Character	Due to regression 1 d. f.	Residual 76 d. f.
Height-leaf length ratio		
Blocks 1-3	760,811**	251
Blocks 4-6	706,251**	380
Leaf drop		
Blocks 1-3	20,877**	7
Blocks 4-6	22,765**	7
Multiple stem frequency		
Blocks 1-3	5,500**	68
Blocks 4-6	1,701**	53
Adjusted stem diameter		
Blocks 1-3	4,680**	2
Blocks 4-6	4,069**	2
Adjusted stem height		
Blocks 1-3	88,837**	86
Blocks 4-6	64,732**	86

**Significant at .01 level.

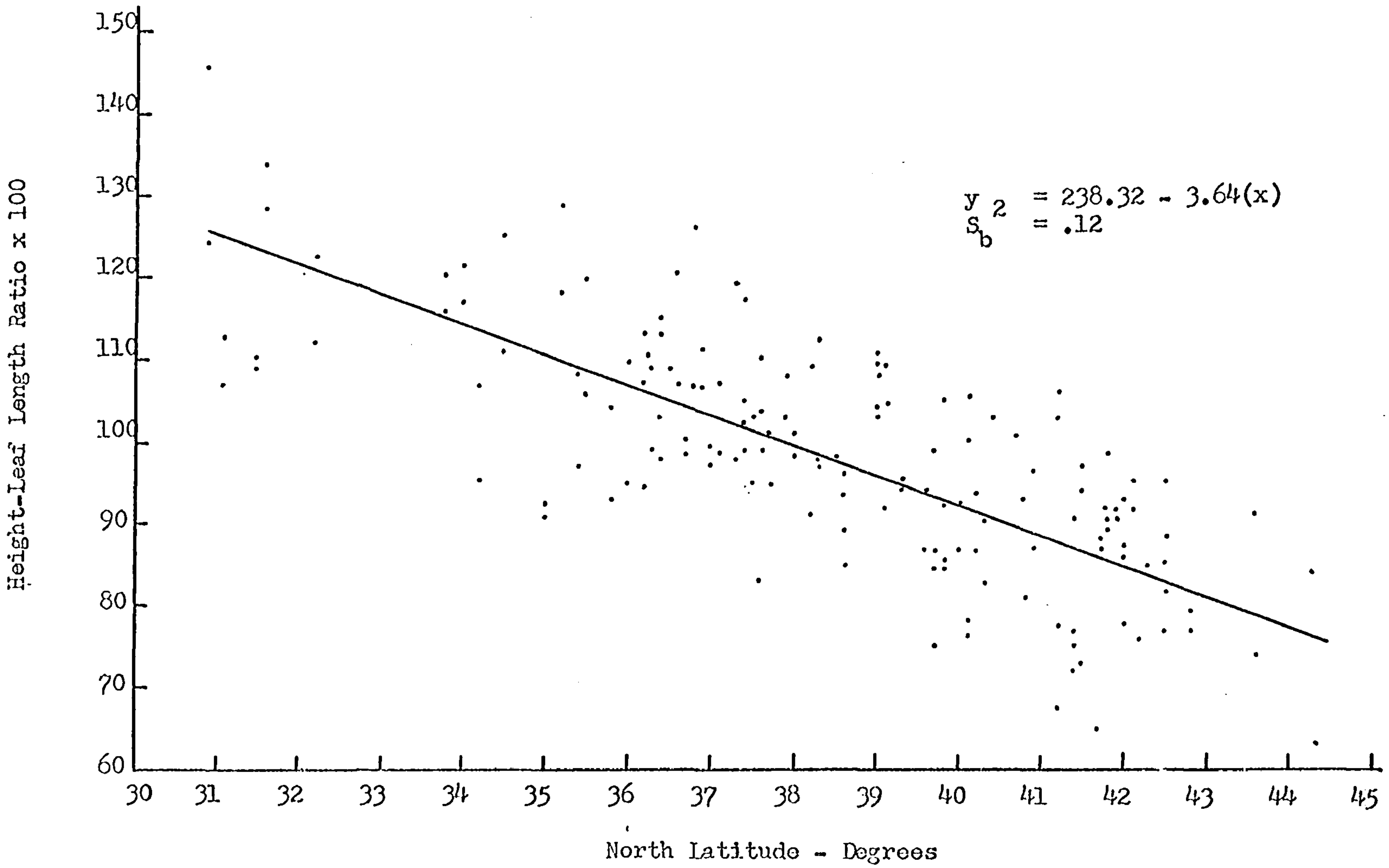

Figure 6. The relationship of height-leaf length ratio and latitude of seed source

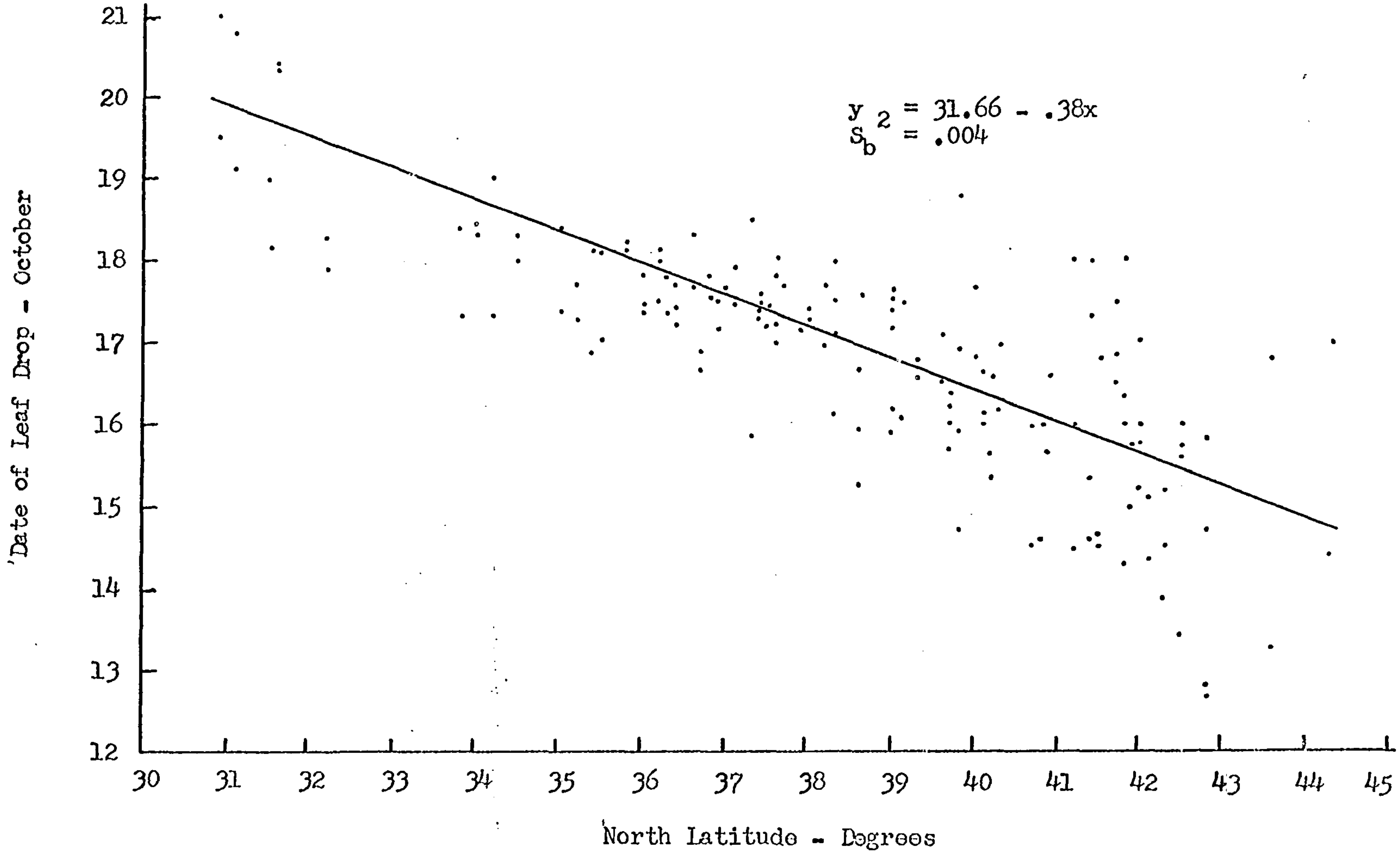

Figure 7. The relationship between date of leaf drop and latitude of seed source

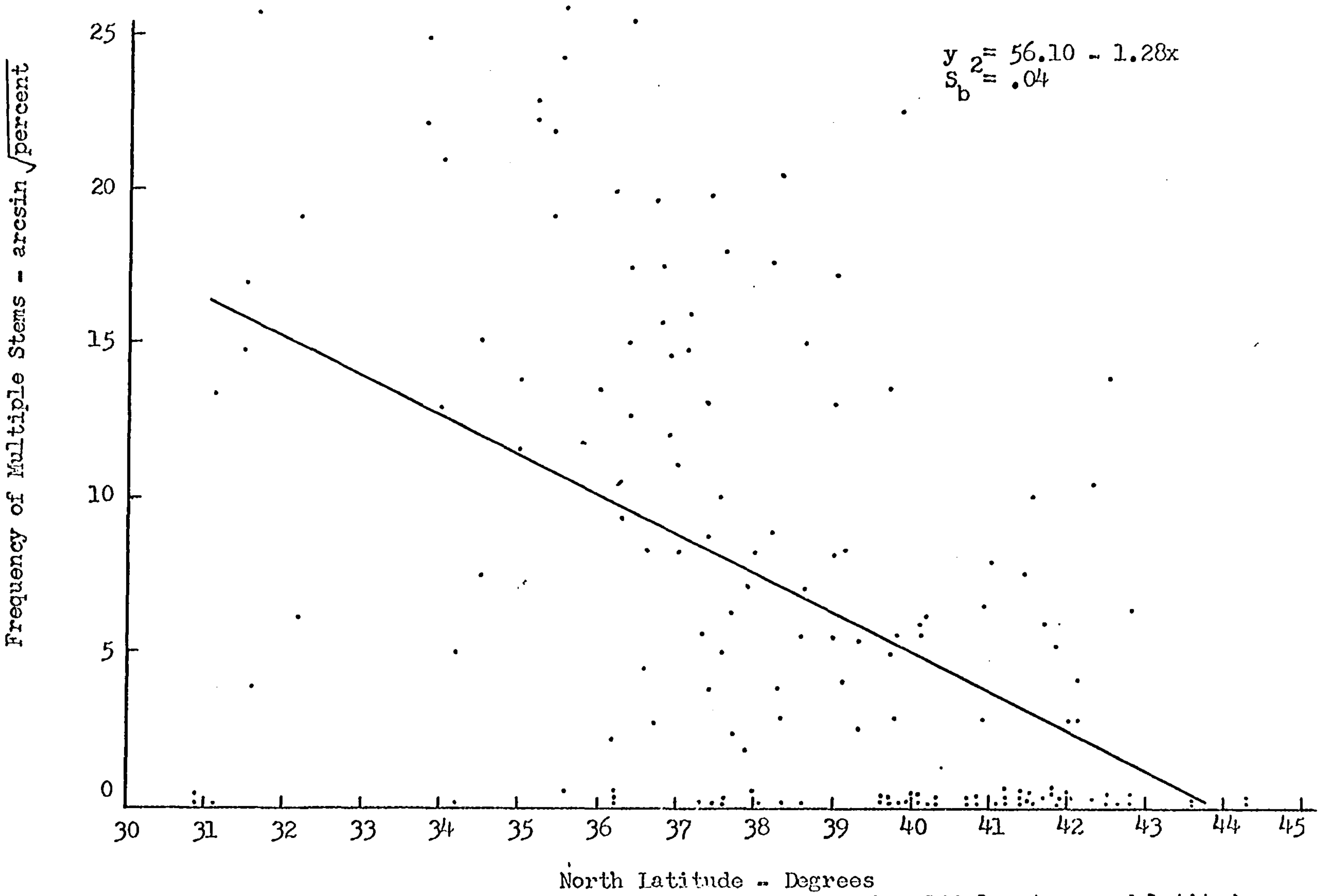

Figure 8. The relationship between frequency of trees with multiple stems and latitude of seed source

data was $y = 56.10 - 1.28x$. The variance of the sample regression coefficient was .04.

Adjusted stem diameter

There were a large number of differences between sources for adjusted stem diameter. The values were plotted on a graph and there appeared to be a linear north-south trend. Blocks 1-3 were analyzed using linear regression. The regression was significant at the .01 level (Table 4).

Using data from blocks 4-6, a regression was run using the linear model developed from blocks 1-3. The regression was significant at the .01 level. Data from blocks 1-6 were pooled for a better overall estimate of the slope (Figure 9). The regression equation for the combined data was $y = 13.57 - .16x$. The variance of the sample regression coefficient was .001.

Adjusted stem height

There were a large number of differences between sources for adjusted stem height. The values were plotted on a graph and there appeared to be a linear north-south trend. Blocks 1-3 were analyzed using linear regression. The regression was significant at the .01 level (Table 4).

Using data from blocks 4-6, a regression was run using the linear model developed from blocks 1-3. The regression was significant at the .01 level. Data from blocks 1-6 were pooled for a better overall estimate of the slope (Figure 10). The regression equation for the combined data was $y = 118.27 - 2.25x$. The variance of the sample regression coefficient was .05. Sources from Texas and Mississippi appear to be growing at a rate comparable to those sources from about 38° N latitude. This suggests

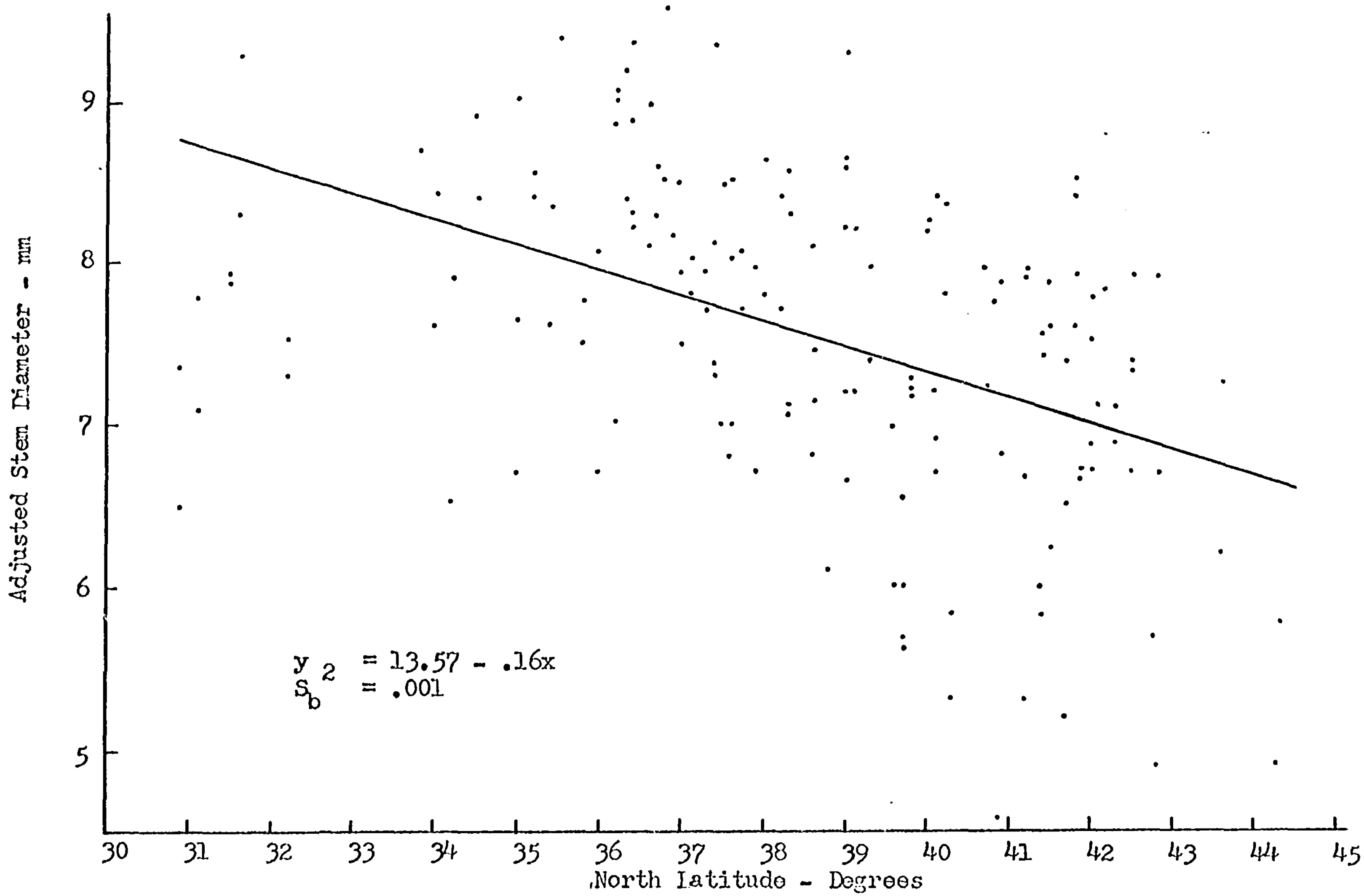

Figure 9. The relationship between adjusted stem diameter and latitude of seed source

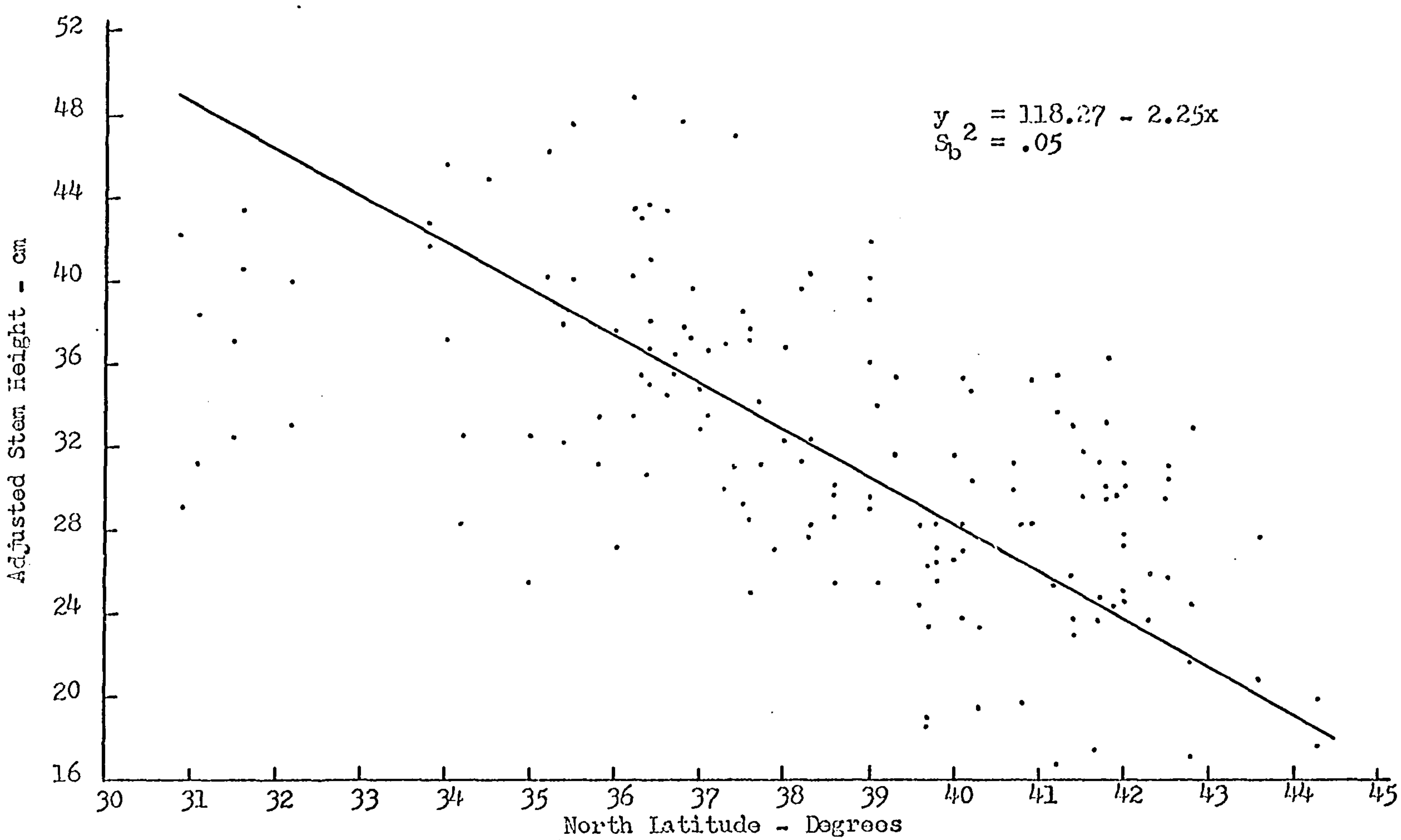

Figure 10. The relationship between adjusted stem height and latitude of seed source

that the extreme southern part of the range may not be the best source of genes for rapid growth.

Variance Components, Coefficient of Variation and Heritability

An analysis of variance was run using all six blocks in the experiment for the purpose of estimating the variance components for each character. The analysis of variance with the expected mean squares is presented in Table 5.

The within source variances or family variances (σ_F^2) and the between source variances (σ_S^2) were computed as follows:

$$\sigma_F^2 = \frac{\text{Family MS - B x Family MS}}{\text{blocks}}$$

$$\sigma_S^2 = \frac{\text{Source MS - B x Source MS}}{\text{blocks}}$$

Both family and source variance components were then computed as a percentage of the B x family MS. By using the percentage values, more meaningful comparisons between characters can be made (Table 6).

For the eight seedling characters studied, the average variance percentage for families and sources was 7.9 and 49.6 respectively. As would be expected, source variance exceeds the family variance for each character. The relative variance percentages vary by character.

The coefficient of variation (CV), a relative measure of variation, was computed for each character, using all six blocks (Table 6). The values ranged from 11.3 percent for leaf drop to 186.7 percent for multiple stem frequency. All other characters, except insect damage (50.4 percent) varied between 15.1 and 26.2 percent.

Table 5. Analysis of variance with expected mean squares used for determining the variance components

Source of variation	Degrees of freedom	Expected mean square
Blocks - B	b - 1	
Sources - S	s - 1	$\sigma_e^2 + b\sigma_F^2 + f\sigma_{BS}^2 + b\sigma_S^2$
B X S	(b-1)(s-1)	$\sigma_e^2 + b\sigma_F^2 + f\sigma_{BS}^2$
Families-in-sources-F	s(f-1)	$\sigma_e^2 + b\sigma_F^2$
B X F	(b-1)(s)(f-1)	σ_e^2

The narrow-sense heritability (H) for seedling characters was computed from the partitioned variances as follows:

$$H = \frac{2\sigma_F^2}{\frac{\sigma_e^2}{b} + 2\sigma_F^2}$$

The doubling of female (family) effects was done on the assumption that the unknown male effects would be equal to the tested female effects. The majority of the parent trees were unselected, and the assumption of male effects equaling female effects is very likely true.

Heritability values for seedling characters ranged from .22 for leaf drop to .66 for adjusted stem diameter (Table 6). Leaf color and adjusted stem height were comparatively high, .62 and .61 respectively. Heritabilities for other characters varied from .30 to .48.

Heritability for seed weight was estimated using the formula,

Table 6. Family and source variance (as percent of Block x Family variance), mean for all sources, coefficient of variation, and heritability for nine characters studied

Character	Family variance	Source variance	Mean for all sources
	percent	percent	
Leaf color	13.7	52.6	3.44 (rating)
Insect damage	6.3	28.3	3.32 leaves
Leaf angle	7.8	25.8	2.99 degrees (coded)
Height-leaf length ratio	7.2	71.4	99.48 (ratio)
Leaf drop	2.4	73.8	16.94 (October date)
Multiple stem frequency	3.6	18.2	10.47 (arcsin percent)
Adjusted stem diameter	16.2	53.2	7.72 mm
Adjusted stem height	13.0	73.6	35.19 cm
Nut weight	28.2[a]	8.7[a]	22.36 g

Character	Coefficient of variation	Heritability value
	percent	
Leaf color	15.1	.62
Insect damage	50.4	.43
Leaf angle	18.6	.48
Height-leaf length ratio	20.2	.42
Leaf drop	11.3	.22
Multiple stem frequency	186.7	.30
Adjusted stem diameter	20.1	.66
Adjusted stem height	26.2	.61
Nut weight	23.7	.76[b]

[a]Family and source variance, *per se* (no block interaction).

[b]Computed as family variance/total variance.

$H = \dfrac{\sigma_F^2}{\sigma_F^2 + \sigma_S^2}$; where σ_F^2 and σ_S^2 are family and source variance respectively. Heritability was computed as .76. The heritability value is undoubtedly somewhat inflated. No sampling error for within families was included in the denominator. Any increase in the total variance would obviously decrease the heritability.

Correlation between Characters

General procedure

Using the data from all six blocks, the correlation coefficients (r values) between all characters were computed (Table 7). The r values were based on observations in 1840 plots. The following formula was used to test the null hypothesis that the correlation values were equal to zero:

$$t = \frac{r}{\sqrt{(1 - r^2)/(n - 2)}}$$

At the 5 percent level of significance and ∞ degrees of freedom, r is computed to be .04. All r values greater than +.04 and less than -.04 are then significantly different from zero.

The distinction between significance and meaningfulness can be a serious problem. Although small values turn out to be significant, they may or may not be meaningful. The correlation values will be discussed in terms of trends suggested.

Leaf color

All correlations between leaf color and other variables were negative.

Table 7. Correlation coefficients between eight characters

Character	Character a	b	c	d	e	f	g	h
a - Leaf color	X							
b - Insect damage	-.02[a]	X						
c - Leaf angle	-.03	.00	X					
d - Date of leaf drop	-.08	.06	.00	X				
e - Height-leaf length ratio	-.06	.27	-.07	.20	X			
f - Multiple stems	-.09	.17	.07	.15	.15	X		
g - Adjusted stem diameter	-.07	.41	-.10	.04	.46	.17	X	
h - Adjusted stem height	-.09	.41	-.09	.07	.69	.22	.82	X

[a] All r values greater than +.04 or less than -.04 are significantly different from zero.

Leaf color was estimated as the degree of greenness in the new leaves. Plants with all new red leaves were coded "1" with gradations to all new leaves being coded "5". The correlations between leaf color and insect damage, and leaf color and leaf angle were not significant. In terms of trends, the trees on which new leaves are red tend to be faster growing, lose their leaves later, have relatively shorter leaves, and have a higher frequency of multiple stems. Although cause and effect is not suggested here, a possible hypothesis is that red leafed trees tend to be more photosynthetically efficient. Other tests would be necessary to show this. It should be pointed out that the red colored new leaves are associated with geographic sources in southeastern United States, and this in turn accounts for the growth differences.

Insect damage

Insect damage, as measured by the number of chewed leaves per tree, was positively correlated with leaf drop date, height-leaf ratio, multiple stem frequency, stem diameter and stem height. Plants which grew larger were more susceptible to the insect attacks than were the smaller plants. It is possible that the larger plants simply had more leaves to be chewed on than did the smaller plants. The developmental stage of the plants may also have been an influencing factor. Germination of some seeds was delayed for several weeks, and the late germinators would not have had as much exposure time to the insects as the early germinators. There was no correlation between insect damage and leaf angle.

Leaf angle

Leaf angle is positively correlated with the frequency of multiple stems. The plants with the widest leaf angle also had the highest frequency of multiple stems. Since the correlation is low (.07) and since multiple stem tendencies are likely the result of damage to the terminal bud, the correlation is probably not meaningful in terms of selection. Leaf angle is negatively correlated with the height-leaf length ratio, stem diameter, and stem height. This means that by selecting for trees with a wide leaf angle, we are concomitantly selecting for trees with a low height-leaf length ratio and low height and diameter. It has been suggested that wide leaf angle, relatively short leaves, and rapid height and diameter growth are all desirable traits. Because of the negative correlations between these characters, genetic gains may be reduced. However, it is possible that the fast growing trees are from one region and wide leaf angled trees from another. This situation would confound the overall correlation. Barber (1964) has shown that in slash pine (*Pinus elliottii* Engelm) branch length and diameter are negatively correlated with branch angle.

Date of leaf drop

Date of leaf drop is positively correlated with insect damage, height-leaf length ratio, frequency of multiple stems, stem diameter, and stem height. Date of leaf drop is indicative of the onset of dormancy. Those plants that drop their leaves last are also the last to stop growing in the fall. There was no correlation between date of leaf drop and leaf angle. Plants which continue growth longest in the fall (the southern sources) apparently do not have any wider or narrower leaf angle than plants which stop growth early in the fall (the northern sources).

Height-leaf length ratio

A high height-leaf length ratio indicates relatively taller plants or shorter leaves, and is considered to be a desirable attribute. It is positively correlated with insect damage, leaf drop date, multiple stem frequency, stem height, and stem diameter. It is negatively correlated with leaf color and leaf angle. Since height is a component of the height-leaf length ratio, it is not surprising that the correlation with stem height is somewhat higher than the correlation with stem diameter. High height-leaf ratios associated with high insect damage, high multiple stem frequency, and low leaf angle will make a selection program difficult and cause a reduction in expected genetic gains.

Multiple stems

Multiple stems frequency was positively correlated with all characteristics except leaf color. Plants with multiple stems are also susceptible to chewing insects. Insects were observed chewing the tips out of some trees and are presumed to be the agent responsible for causing multiple stems. A high multiple stem frequency is also associated with wide leaf angles, late leaf drop, high height-leaf length ratio, stem diameter and stem height.

Stem diameter

Stem diameter is positively correlated with stem height (.82). Seedlings with a caliper (diameter) of 1/4 inch or more at one inch above root collar are most desirable as planting stock. Survival is higher and growth is more rapid when large stock is used. Although there is a high correlation between height and diameter here, the correlation may not be as high under standard nursery practices. Nursery trees are grown under much denser conditions, that tend to promote a taller tree with a smaller diameter.

DISCUSSION

The Pattern of Variation

The pattern of variation for most characters in black walnut is continuous, not ecotypic. Distinct geographic races of walnut apparently do not exist. Variation in several characters was associated with latitude. Climatic, biotic, and edaphic factors that are associated with latitude are apparently the major forces of natural selection on the species. The biotic and edaphic factors are interrelated and also partially dependent on the climate. Some climatic factors that may be associated with the general pattern of variation include average annual precipitation, average annual minimum temperature, average high summer temperature, annual temperature range, and photoperiod. Length of growing season is dependent on these climatic factors and is also correlated with latitude. The components of climate that are listed have a general directional change from north to south (Visher 1954). The major seed-collection zones for trees of central United States generally follow the latitude lines (Limstrom 1965).

It has been shown that black walnut from various geographic areas are gentoypically different. Black walnut has probably evolved from Juglans olanchana which originated in Central America (Manning 1957). The natural botanical range of black walnut has and probably still is moving northward. The ability to withstand the cold, probably limits the extension of the range to the north. Mutation and recombination of alleles initially provide the variants (new genotypes) on which the forces of selection operate to extend the natural range. Obviously, mutations and recombinations are still occurring in all parts of the range.

As compared with northern sources, a southern source of the same species is usually faster growing, capable of growing long in the autumn, less susceptible to late spring or early autumn frosts, and more susceptible to damage by winter cold (Wright 1962). It is the author's opinion that through a tree improvement program, the range of walnut can be extended northward and that faster growing varieties from the more southern part of the range can be moved north. The most efficient procedure for selecting for rapid growth may be to plant southern sources in the north and screen for winter-hardiness. Hopefully, the genes for rapid growth will be linked to the genes for winter-hardiness. Genotypes with the winter-hardy adaptation will certainly remain undiscovered if grown only in the southern part of the range.

There is evidence that the range of black walnut can be extended to the north. Ellis (1925) reported that black walnut seedlings of west-central Illinois origin thrived for 60 years in west-central Vermont, approximately 200 miles north of their origin. A. J. de Lotbiniere (1920) reports that a walnut plantation in Quebec, Canada reached 55 feet in height and 7 inches in diameter in 37 years. Dr. L. Parrot[1] reports that there are old plantations of black walnut growing near Quebec, Canada. The source is unknown, but Quebec is approximately 250 miles north of the nearest part of the natural range. The author knows of walnut growing in Houghton County and Alpena County, Michigan; they are about 200 and

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[1]Parrot, L. Department of Forestry, Universite Laval, Quebec, Canada. Personal communication in letter concerning seed exchange. 1967.

100 miles, respectively, north of the boundary of the natural range.

The previous examples of extension of the walnut range are not sufficient evidence to recommend that southern seed sources be used exclusively. Until experiments show otherwise, it will be wise to use local sources for reforestation purposes. Nevertheless, where high yield is an important attribute, considerable effort in a tree improvement program should be devoted to selecting winter-hardy trees from the southern part of the range.

Variance Components, Coefficient of Variation and Heritability

Family variance and source variance expressed as a percent of the block x family variance provides a means whereby variances between characters can be compared. However, the total (family plus source) variance percentage must be considered when making comparisons between characters. For some characters, the family and source (combined) variance percentage will be low. A low combined variance percentage indicates that the interaction (block x family) is relatively high; whereas a high combined variance percentage indicates that the interaction value is relatively low. Leaf color, height-leaf length ratio, leaf drop, adjusted stem diameter, and adjusted stem height have relatively high family and source (combined) variance percentages while insect damage, leaf angle, and multiple stem frequency have low variance percentages.

Leaf color, height-leaf length ratio, leaf drop, adjusted stem diameter and adjusted stem height have source variance percentages of more than

50. The ratio of family to source variances for height-leaf length ratio and leaf drop was 1:9 and 1:30 respectively. For all other characteristics, the ratio of family to source variances was 1:3 to 1:5. For height-leaf length ratio, leaf drop, and adjusted stem height, selection emphasis should be on sources rather than families. For leaf color and adjusted stem diameter, more concern should be on family selection. And for insect damage, leaf angle, and multiple stem frequency, still less concern should be on source selection.

Leaf drop variance percentage for source is much higher than for families. Leaf drop, which is indicative of the onset of dormancy, is influenced by photoperiod. Pauley and Perry (1954) reported that cessation of shoot growth in Populus was related to day length of the seed source. Selection for late leaf drop (longer growth or late dormancy) would be most effective by selecting sources rather than families.

Family variance percentage for adjusted stem diameter was slightly higher than family variance percentage for adjusted stem height. In contrast, the source variance percentage for adjusted stem height was higher than source variance percentage for adjusted stem diameter. About 90 percent of the sources in the study originated from areas south of the testing area. As a result, most of the sources would be expected to grow until late in the fall. Diameter growth normally continues longer into the fall than height growth, and differences in diameter between sources apparently become smaller. There must be a differential growth rate between sources as related to time. As a result the source variance percentage for diameter growth decreases. However, the family variance percentage for diameter increases, apparently due to increased differences in diameter growth with time.

Family variance for nut size was more than three times as large as the source variance. Emphasis in selection for nut size should be on an individual tree basis, rather than selecting sources from broad geographic areas.

The coefficient of variation values may be useful when designing future experiments. High CV values, such as that for insect damage and multiple stem frequency, suggests that a large number of replications would be needed to get significant differences at a given level of probability; whereas where the CV is low fewer replications would be needed to get significance at the same probability level. A high CV value also suggests that the measuring technique (selection screen) needs to be refined. Most of the characters measured have CV values of about the same magnitude as agronomic crop values. CV values from 10 to 25 percent are common for yield data of agronomic crops (LeClerg 1966).

The heritability values for the seed weight and seedling characters are approximately the same magnitude as the heritability values of characters in agronomic crops (Gardner 1963). In general where heritability is high, the improvement program should employ mass selection. As the heritability becomes lower, more emphasis should be placed on progeny testing and hybridization.

Heritability may be used to estimate expected improvement due to selection. However, general heritabilities for a given characteristic may be extremely variable. They vary due to the plot size, density and number of replications and must be used with caution for prediction purposes (Robinson 1963).

PART II. APICAL DOMINANCE IN BLACK WALNUT

THE PROBLEM AND STUDY OBJECTIVES

A walnut log must be straight and free of defect to be classified as veneer quality material. Crookedness in mature trees is undoubtedly related to deformities that develop during the juvenile growth period. The causes of crooked walnut stems are many and variable. High winds, ice storms, low winter temperatures, late spring frosts, insects and other animals can damage or destroy the terminal shoot. In any case, a lateral branch or bud must rapidly assume a terminal (dominant) position if the tree is to have the straight stem necessary for veneer-quality logs. Young walnut trees in plantations exhibit a variety of forms. When the terminal shoot is killed and no lateral branch assumes the dominant position, a bushy or apple-tree form is the result. In other cases, a single lateral branch will assume a vertical position and a straight-stemmed tree will develop. It appears that the failure of lateral shoots to assume a dominant position is a major reason for stem crookedness.

Since stem-straightness is partially dependent on the growth and development of lateral buds, it seems logical to hypothesize that some components of apical dominance might also be related to stem straightness. Phototropic response, leaf angle, leaf length, and bud suppression or some combination of these might be the "screen" that would provide for the selection of seedlings that are genetically superior in their ability to form straight stems. Whether or not the seedling selection is effective will depend on the amount of natural variation present in the seedling population and the degree of correlation between seedling responses and the stem-straightness of mature trees. This study is aimed at determining the amount of natural variation present in a seedling population.

The objectives of this study were to determine the magnitude of differences in epicotyl curvature (response to unilateral light), leaf angle and height-leaf length ratio for six black walnut seed sources from widely separated latitudes.

REVIEW OF LITERATURE

The apical-dominance phenomenon implies that the shoot apex inhibits the growth and development of the lateral buds. The inhibitory action is widespread throughout the plant kingdom. Apical-dominance phenomena may be grouped into three classes: inhibition of branching, regulation of which branches will grow more rapidly than others, and control of branch angle (Leopold 1964). Auxin is involved in all three classes of apical-dominance. Apical dominance is probably due to an interaction or balance between auxin and kinin (Wicksom and Thimann 1958; Kefford and Goldacre 1961).

Phototropism refers to the bending of plant shoots in response to unilateral illumination. Briggs (1963), and Pickard and Thimann (1964) have shown that light causes auxin to move from the lighted to the shaded side of corn coleoptiles. The auxin differential is considered to be the primary cause of shoot bending.

Karschon (1949) has shown that scotch pine seedlings of low Swiss elevation showed stronger phototropism than seedlings from the mid or higher elevations. He also showed that seedlings from eastern Europe showed a weaker phototropic reaction than did those seedlings from western Europe. Schmidt (1932) found a similar east-west gradient and also a north-south gradient. Seedlings from the North and West showed a stronger phototropic response than did seedlings from the South and East. Schmidt showed that early phototropic seedling response was correlated with later stem straightness. The experiments of both Karschon and Schmidt dealt with the curvature of the stem.

Schrock (1958) showed that pine seedlings with a weak phototropic response developed straighter stems than those with a strong response. The response was measured in terms of the curvature of the hypocotyl after a 35 minute exposure to 440 watt quartzlight. A large number of plants were tested in this experiment and considerable variation was observed. Some promising straight-stemmed plants were found.

Work with soft maples in the Northeast revealed a wide variation in percentages of trees that recovered good stem-form after being cut back (topped). Particularly noteworthy were the comparatively high percentages of good-form-trees resulting from a particular male parent (United States Department of Agriculture 1965b). This work suggests that stem-form (stem-straightness) might be under strong genetic control.

MATERIAL AND METHOD

Seed Handling, Seedling Development, and Treatment of Material

The nuts for this study were collected in the fall of 1965. They were cleaned, placed in plastic bags, and stored in the seedling storage shed at the Iowa Conservation Commission nursery. They were put in storage November 15, 1965. The temperature in the storage shed was 2° C. throughout the winter. The nuts were taken out of storage on April 21, 1966. Within two days, the nuts began germinating. Within six weeks a sufficient number of nuts for this study had germinated.

When the hypocotyl had emerged 0.5 to 1.0 cm, the germinating nuts were split longitudinally. Genetically identical pairs of seedlings can be produced using this procedure (Bey 1967). By using genetically identical material we are able to make comparisons between pairs. A pair consists of two seedlings of identical genotypes. Each half was placed in a Jiffy peat-pot filled with a mixture of one-third sand, one-third soil, and one-third peat. An identification label was put in each pot. The pots were placed on a table under a 200-watt incandescent light, and watered once a day. When the epicotyl had emerged about 1 cm and the epicotyl hook had straightened, the seedlings were moved to a dark room. Preliminary investigation indicated that the epicotyl hook would not straighten before the seedlings were 7 cm tall if they were started in a dark room. The 200-watt incandescent light apparently provided sufficient stimulus to straighten out the hook. Most of the seedlings exposed to the 200-watt bulb had straight stems. In a few cases, the seedlings were bent toward the side of the plant, which had been cut in the splitting process. Where scarred tissue and bending was very pronounced, the stem was severed at ground line and a new shoot was allowed to develop.

Two research difficulties were encountered during the early phase of this experiment. They were (1) what quality of light to use, and (2) what dosage of light to use.

The Bunsen-Roscoe reciprocity law states that if light intensity and time of exposure are varied in such a way that the product of the two remains constant, the photochemical effect of the light should also remain constant. This has been shown to be valid for corn and oat coleoptiles with unilateral white light for dosages of 1,000 meter-candle-seconds (mcs) or less (Briggs 1960). Zimmerman and Briggs (1963) stated that the reciprocity laws are valid for first positive and first negative curvature but the second positive curvature is a linear function of exposure time, and independent of intensity.

A small test was run to determine if the second positive curvature was a linear function of exposure time. The light source, a 300-watt incandescent bulb, was placed 23 cm from the seedlings, for varying lengths of time to get light dosages of 5,000, 10,000, 20,000, 40,000, and 80,000 mcs. The same procedure was followed using a 15-watt fluorescent Gro-lux light. The seedlings were placed 9 cm from the light. Five seedlings were treated for each light dosage and each type of light. The seedlings were returned to a dark room and the curvature was measured one, two, four, eight and twenty-four hours after treatment.

The objective was to determine the quantity and quality of light which gave the maximum response. Variation in maximum response could then be measured. I expected that with both the fluorescent and the incandescent light, the curvature would increase gradually to its maximum and then decrease and stop. After measuring the response of about 50 seedlings over an 8-hour period, I found that this was not true. In nearly every case there was a rhythmic response. The seedlings first bent toward the side which was lighted and then back away from the lighted side (to the pretreatment position). The frequency of the alteration varied but many seemed to be on a two- to three-hour cycle. It appeared that maximum curvature could be measured between 1 and 2 hours after exposure. In order to pinpoint the maximum exposure more precisely, curvature measurements were made on a new group of seedlings at 15 minute intervals over the first 2 1/2 hour period. Dosages of fluorescent light of 10,000 mcs and 20,000 mcs and dosages of incandescent light of 20,000, 40,000, 60,000 and 80,000 mcs were used. The maximum response time varied with the light dosage. A rhythmic pattern prevailed under all dosages used. The 60,000 mcs dosage was selected, because it gave the least erratic results. Maximum response occurred after 60 minutes. It was obtained by placing a 300-watt bulb 29 cm from the seedling for 20 minutes.

The incandescent light was selected for two reasons. First, incandescent light quality is more like that of the sun light than is fluorescent light. Fluorescent light has a higher proportion of blue light (shorter wave lengths). Second, stem curvature seemed to be more erratic using fluorescent light. It appeared that we were getting a first positive, first negative, and second positive curvature. Several of the stems exposed actually had an S-shaped form at sometime during the 8-hour measurement period. It is very difficult to measure this kind of curvature.

Each seedling was placed in a black box, about 20 cm square, with a slit 2 mm wide on one side. A flat, plastic stake (1 cm wide and 15 cm tall) was placed next to the seedling to indicate the seedling's pre-treatment position. After treatment (exposure), each seedling was returned to the dark room.

After 60 minutes in the dark room the curvature of each seedling was measured. After the epicotyl curvatures were measured, the seedlings were placed under a 200-watt incandescent light for one day. In the time of one day the seedlings turned from pale yellow to a light green color. The seedlings were then transplanted to 5.4 liter painted metal cans and set out at the Iowa Conservation Commission Nursery. The cans were filled with a mixture of one-third sand, one-third peat, and one-third loam soil. Some of the tender and succulent seedlings were killed by the sunlight and heat, despite attempts to shade the seedlings. In some cases the top was killed back and the seedling resprouted. The seedlings were watered three times each week throughout the summer.

Measurements on leaf angle, height, and leaf length were made on August 22, 1966. Height growth had stopped by that time. In October 1966, the seedlings were lifted from the pots, packaged, and placed in a cooler for the winter. In April 1967, the seedlings were renumbered and planted in a completely randomized block design. Three hundred and twenty-two seedlings were planted at a one-foot by one-foot spacing. Height, leaf length, and leaf angle were measured in July 1967.

Experimental Design

A randomized complete block design was used in the laboratory and nursery the first year. Three blocks were used. Each block contained six sources, three families per source and at least two pairs per family. These seedlings were used to estimate the genotypic variation for epicotyl curvature, leaf angle, and height-leaf length ratio.

The six sources were selected from six widely different latitudes in a narrow longitudinal band over the range of the species (Table 8).

Table 8. Table of number, code, and location of six sources included in the study

Local stand no.	Source code	County and state	North latitude		West longitude		Elevation
			Degrees and minutes				Meters
2502	1	Winona, Minnesota	44	10	91	50	210
1803	2	Delaware, Iowa	42	20	91	17	275
2705	3	Marion, Missouri	39	39	91	25	201
2704	4	Dent, Missouri	37	30	91	40	357
1101	5	Stone, Arkansas	35	50	92	20	366
3904	6	Walker, Texas	30	50	92	25	107

An attempt was made to use trees which had nuts of approximately the same size. However, because of low germination in some lots, it was not possible to adhere to the uniform nut size requirement. Average weight per nut by family ranged from 16.3 to 33.9 grams.

Data Collected

Epicotyl curvature

Epicotyl curvature was measured on each seedling one hour after being exposed to a 60,000 mcs dosage of incandescent light. The seedlings were in a dark room for the one hour before measurement. The curvature was measured in an indirect light supplied by a 15-watt bulb. A protractor was placed behind each seedling and the 0° line was aligned with the previously set plastic stake. The stake indicated the seedling's pre-treatment position. The curvature was measured to the nearest degree as the deviation of seedling tip from the pre-treatment position (Figure 11).

Leaf angle

Leaf angle was measured on the two longest leaves on each seedling. The two leaves had to be located at least 90° apart (around the stem) to be measured. The angle was measured from the leaf base to mid-point on the leaf rachis (Figures 12 and 13). The average angle for the two leaves was recorded to the nearest five degrees.

Leaf length

Leaf length was measured on the two longest leaves on each seedling. The two leaves had to be located at least 90° apart (around the stem) to be measured. The average length for the two leaves was recorded to the nearest centimeter.

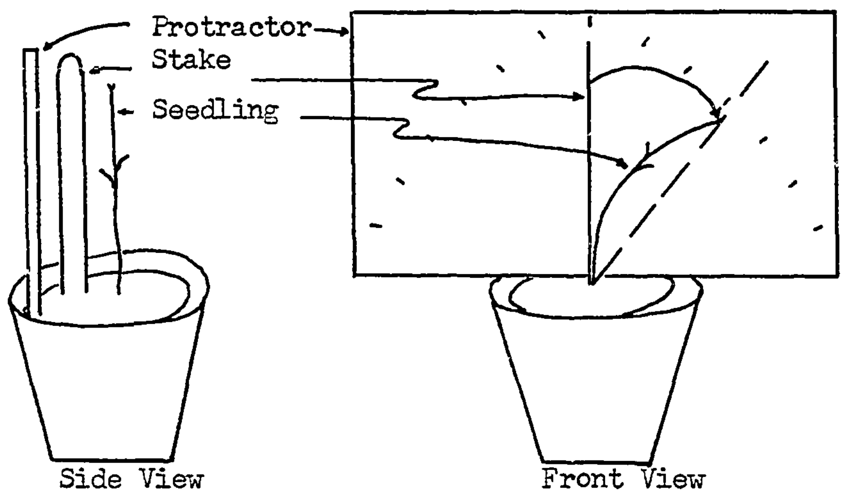

Figure 11. Epicotyl curvature was measured with a protractor as deviation of the seedling tip from the pre-treatment position.

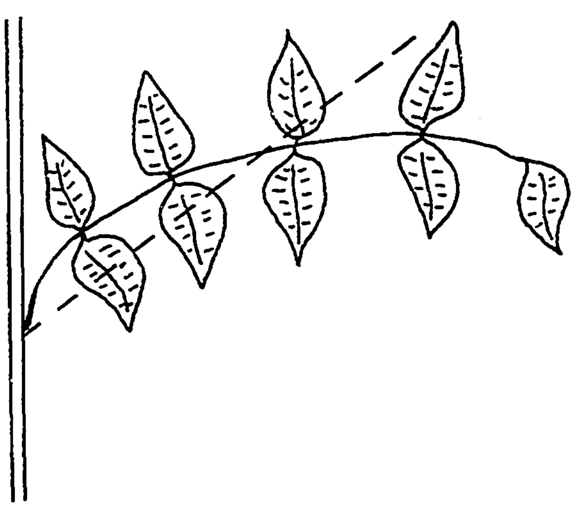

Figure 12. Leaf angle was measured from the leaf base to mid-point on the leaf rachis.

Figure 13. Leaf angle was measured on paired seedlings. Note similarity within pairs and difference between pairs.

Stem height

Total stem height was measured to the nearest centimeter after height growth for the season had stopped. Terminal bud formation was considered to be indicative of height growth cessation.

RESULTS

First Year Data

Epicotyl curvature

Epicotyl curvature was measured and analyzed on 258 seedlings in 17 different families. Seedlings which had crooked stems or were more than 7 cm tall were not exposed to the unilateral light and consequently were not measured. Only seedlings which contained both seedlings of a pair were measured and used in the analysis.

There were significant differences between pairs of seedlings (Table 9). Tukey's w-procedure was used to determine the critical values. Pairs which differed by 16.2 degrees or more are considered significantly different. Curvature on individual seedlings ranged from negative 12 degrees to a positive 30 degrees. Negative curvature refers to a bending of the stem away from the source of light, while positive curvature refers to a bending toward the source of light.

There were no significant differences between sources or families. The average curvature by source varied from 3.0 degrees for source 3 in Marion County, Missouri to 6.1 degrees for source 6 in Winona County, Minnesota (Table 10). The average curvature for families varied from 1.2 degrees for family 302 in Marion County, Missouri to 6.0 degrees for family 103 in Winona County, Minnesota.

Leaf angle

Leaf angle was measured on August 10, 1966. Terminal buds had formed and height growth had ceased for the season. Three hundred and

Table 9. Mean squares from analyses of variance for sources, families and pairs of seedlings for epicotyl curvature, leaf angle and height-leaf length ratio

Character	Source	Family	Pairs
Epicotyl curvature	41.0^{NS}	8.3^{NS}	36.8*
Leaf angle - first year	178.4^{NS}	64.7^{NS}	136.6*
Leaf angle - second year	100.0*	49.7^{NS}	40.1^{NS}
Height-leaf length ratio - first year	1,361.2*	251.8^{NS}	635.8^{NS}
Height-leaf length ratio - second year	5,755.8*	458.1*	204.6^{NS}

*Significant at .05 level.

^{NS}No significant differences at .05 level.

ten seedlings were used in the analysis.

The analysis of variance revealed significant differences between pairs (Table 9). Pairs which differed by 22.8 degrees or more are significantly different. Leaf angle varied from 30 to 70 degrees for individual seedlings.

There were no significant differences between families or between sources. Family averages ranged from 35.8 degrees for family 604 in Walker County, Texas to 58.7 degrees for family 102 in Winona County, Minnesota (Table 10). Source averages ranged from 43.2 degrees for source 6 in Texas to 49.0 degrees for source 1 in Minnesota.

Height-leaf length ratio

Stem height and leaf length were measured on 288 seedlings on August

Table 10. Average epicotyl curvature, leaf angle and height-leaf length ratio by families and sources for one-year old seedlings in pots

Family number	Epicotyl curvature	Leaf angle	Height-leaf length ratio
	Degrees	Degrees	
102	3.0	58.7	102.2
103	6.0	48.6	96.5
108	7.1	48.8	94.3
Source 1 average	6.1	49.0	95.9
206	4.1	45.0	77.5
210	5.1	45.0	82.6
212	5.1	47.2	100.1
Source 2 average	4.9	46.2	91.5
302	1.2	40.0	93.6
305	3.7	45.8	92.8
310	4.5	49.5	107.3
Source 3 average	3.0	45.6	95.9
401	4.6	45.4	102.9
407	5.0	40.9	94.6
410	3.9	48.1	113.1
Source 4 average	4.4	45.6	105.3
502	4.5	43.7	98.0
504	6.6	44.2	94.5
506	5.4	48.1	92.1
Source 5 average	4.9	44.4	94.8
602	4.6	48.7	95.4
604	1.7	35.8	101.2
Source 6 average	4.1	43.2	97.9
Critical value[a]	- -	- -	- 5.6

[a]Based on Tukey's w-procedure using .05 level.

11, 1966. Ratios were computed for stem height over leaf length x 100. Analyses of variances showed that significant differences in height-leaf length ratios between sources existed (Table 9). Sources which differed by 5.6 units or more are considered significantly different (Table 10). The ratios for sources varied from 91.5 for source 2 in Delaware County, Iowa to 105.3 for source 4 in Dent County, Missouri. Source 4 was different from every other source. Source 2 was different from sources 6 and 4. There were no significant differences between the remaining sources.

There were no significant differences between families or pairs. Family averages ranged from 77.5 for family 206 in Delaware County, Iowa to 113.1 for family 410 in Dent County, Missouri. Individual seedlings varied from 56 to 154 for height-leaf length ratios.

Second Year Data

Leaf angle

Leaf angle was measured on 318 seedlings in the nursery bed on July 12, 1967. The analysis of variance revealed that there were significant differences between sources (Table 9). Sources which differed by more than 3.1 degrees are considered different (Table 11). The leaf angles ranged from 40.7 degrees for source 2 in Delaware County, Iowa to 44.4 degrees for source 6 in Walker County, Texas. Source 2 was different from source 6 and source 1.

There were no significant differences between families or between pairs in families. Family averages ranged from 38.3 for family 206 in

Table 11. Average leaf angle and height-leaf length ratio by families and sources for two-year-old seedlings in nursery

Family number	Leaf angle		Height-leaf length ratio	
	Degrees			
102	43.8		62.2	
103	43.2		64.4	
108	45.0		60.4	
Source 1 average		44.2		62.1
206	38.3		42.5	
210	41.2		59.3	
212	41.0		69.5	
Source 2 average		40.7		62.7
302	42.5		80.2	
305	44.7		59.1	
310	40.6		57.5	
Source 3 average		43.2		62.9
401	42.7		73.5	
407	41.9		73.9	
410	42.7		79.0	
Source 4 average		42.5		75.8
502	40.7		83.4	
504	43.8		81.9	
506	39.4		77.6	
Source 5 average		41.3		80.9
602	47.5		96.7	
604	39.2		91.8	
Source 6 average		44.4		94.9
Critical value[a]	-	3.1	14.3	7.0

[a]Based on Tukey's w-procedure using .05 level.

Delaware County, Iowa to 47.5 for family 602 in Walker County, Texas. Individual seedlings varied from 30 to 60 degrees.

Height-leaf length ratio

Stem height and leaf length were measured on 318 seedlings in the nursery bed on July 12, 1967. The analysis of variance revealed that there were differences between families and between sources for height-leaf length ratios (Table 9).

Families which differed by more than 14.3 units are considered different (Table 11). The family averages ranged from 42.5 for family 206 in Delaware County, Iowa to 96.7 for family 602 in Walker County, Texas. Differences between families with any given source occurred only in source 2 and source 3.

Sources which varied by more than 7.0 units are considered different. The source averages ranged from 62.1 for source 1 in Winona County, Minnesota to 94.9 for source 6 in Walker County, Texas.

There were no significant differences between pairs. Individual seedlings varied from 24 to 145 in height-leaf length ratio.

DISCUSSION

First Year Results

Epicotyl curvature

There were significant differences in epicotyl curvature between pairs of seedlings but not between families or sources. Pairs which differed by 16.2 degrees or more are considered to be different. It appears from this phase of the study that it is not possible to select a superior tree on the basis of the epicotyl curvature of its progeny. The parent trees in this study ranged from good to poor for stem straightness and differences in the epicotyl curvature for the progeny were expected.

The method of handling the seedlings and measuring the curvature may be partially responsible for the erratic measurements within pairs. The maximum difference in curvature within a pair was 20 degrees. In 57 percent of the pairs there was a difference of five degrees or more between individual seedlings of a genetically identical pair. The average difference within pairs was 2.7 degrees. This erratic variation within pairs was not expected. It does point out the need for modifying or refining the technique. There are several extraneous factors which could have affected epicotyl curvature. The seedling pairs were derived by splitting germinating seeds. Although the stem was straight, in some cases it was still possible to see the scarred or cut side of the stem. It was generally partially flattened. No attempt was made to orient this in any particular direction in respect to the unilateral light. It is quite possible that individuals in a genetic pair were oriented differently and consequently exhibited differential growth. The calloused or scarred side would very likely not grow as rapidly as the normal side.

The occurrence of negative bending (away from source of light) was not expected and points to another reason for refining the technique. According to the hypothesis presented before the study was started, no negative bending was anticipated. Negative bending occurs in oat and corn coleoptiles, but only under low light dosages. No explanation for negative bending in this experiment is available.

The response of seedlings to exposure to unilateral light is undoubtedly complicated by the geotropic mechanism operating simultaneously. Brain (1956) found that young Lupinus growing under long day conditions had a stronger geotropic reaction than seedlings growing under short day conditions. The walnut seedlings under study came from widely different latitudes and undoubtedly would have varying genetic constitutions for long and short days. The northern sources would have developed under longer day conditions than the southern sources, and possibly might have stronger geotropic reaction than seedlings from the south.

Alpatova and Moshkov (1962) studied the magnitude of the phototropic and geotropic activity of the shoots of oats, corn, radish, cabbage, tomato, cucumber, buckwheat, and sunflower. The sunflower and radish were most sensitive geotropically. Differences in phototropic sensitivity were insignificant. It was concluded that differences in which way the shoots bend with illumination from one side are caused chiefly by differences in the geotropic rather than the phototropic activity of the plants.

It is interesting to speculate on the mechanism responsible for variation in epicotyl bending. Let us assume that auxin movement and the resulting differential growth is responsible for stem curvature, and that one unit of light will move one unit of auxin across a plant tip. Now suppose that we have two seedlings with 10 and 4 units of auxin in each tip respectively. When one unit of unilateral light is applied to each tip, we would expect one unit of auxin to move across the tip in each case. By assigning units of auxin to each half of the tip, we would have one tip with a 6 and 4 unit distribution and another tip with a 3 and 1 unit distribution--the smallest quantity being on the light exposed side for each tip. The greatest differential (percentagewise) between the two halves occurs on the seedling with the least amount of total auxin. If growth rate for the two seedlings are equal, we would expect the seedlings with the least amount of auxin to be the most sensitive to light and consequently develop into the straightest trees. Schrock (1958) stated that seedlings with a weak phototropic response developed straighter stems than those with a strong response. It is conceivable that the mechanism described above could explain the type of a reaction that Schrock (1958) reported.

However, with a given quantity of unilateral light stimulus, epicotyl curvature is likely to change as the growth rate changes. A rapidly growing seedling, which has a low auxin content (a high auxin differential), would normally exhibit a low degree of epicotyl curvature when exposed to unilateral light. The response could then vary with the growth rate and auxin content.

Leaf angle

Significant differences in leaf angle between pairs and not between families in the first year suggests that we will not be able to select superior parent trees on the basis of the leaf angle of the progeny. However, if wide leaf angle is highly and positively correlated with stem straightness, it might be possible to select superior seedlings.

It appears that individual tree selection for wide branch angle would be more effective than stand selection. The maximum range between sources was six degrees, while the maximum range between families within sources was 13 degrees. Where variation within a geographic area is high compared with variation between geographic areas, emphasis should be on selection within sources rather than between sources. In terms of practical tree improvement, it is often fortunate to have a large amount of variation within stands. Tree improvement programs are often conducted on a state-wide basis where progress, in part, depends on the amount of variation present within the state. A high amount of within-source variation is preferable to a large amount of between-source (between states) variation, where the tree improvement program is confined by state boundaries.

Although the multiple range test revealed no differences between sources, the source averages suggest that there is a trend. Northern sources tend to have a wider leaf angle than do southern sources. The family with the widest leaf angle was from the northernmost source, while the family with the narrowest leaf angle occurred in the southern-most source. It is possible that northern sources will be a better source of genes for wide branch angle than southern sources.

No correlation was run between parent tree stem straightness and leaf angle of the progeny. Stem straightness was reported by cooperators as "good", "average", or "poor". The criteria for straightness depended on the cooperators' knowledge of the stem straightness for the species in the area. For the 17 families under study, the trees classified as "good" (for stem straightness) have wider branch angles than trees classified as "average" or "poor". Parent trees classified as "good" produced progeny with an average leaf angle of 49 degrees while parent-trees classified as "average" and "poor" produced progeny with an average leaf angle of 45 and 46 degrees respectively. Perhaps stem straightness and leaf angle are positively correlated.

Height-leaf length ratio

The height-leaf length ratio is in part an expression of the relative length of the two longest leaves on a plant. Low values indicate relatively long leaves and high values indicate relatively short leaves. Although there were significant differences between sources, there was no apparent north-south trend. Several extraneous factors may have affected the results of the first year data. The seedlings, which were transferred from the laboratory to the field, were succulent and tender as a result of growing in a dark room and the exposure to the field conditions caused dieback in some of the seedlings. Because of the dieback, some of the trees were only a few inches tall at the time of measurement. Walnut seedlings in the nursery would normally be two or three feet tall.

Second Year Results

Leaf angle

Although there were differences in leaf angle between sources, the magnitude of the differences was low. Leaf angle was measured to the nearest 5 degrees and differences of 3.1 degrees were significantly different. Source 2 differed from source 1 and source 6. No north-south pattern of variation was apparent.

The first and second year data for leaf angle are somewhat different and it is impossible to make definite conclusions about leaf angle variation patterns. Although the first year data suggest a weak trend from north to south, the trend is not apparent in the second year data. The within source variation is relatively high as compared with between source variation. I expect that the within source variation would be even greater if trees which where selected for wide branch angle were included as parent trees. From observations on trees in plantations and natural stands, it is apparent that there is considerable variation in branch angle. Trees with wide branch angles are uncommon in all stands. Walnut trees with wide branch angles have a more excurrent form than do trees with narrow branch angles (Figure 14).

Height-leaf length ratio

The relative leaf length decreased from the north to the south. Although there were no significant differences between sources 1, 2, or 3, there were differences between all other combinations. According to the definition of apical dominance presented earlier, the apex of the tree

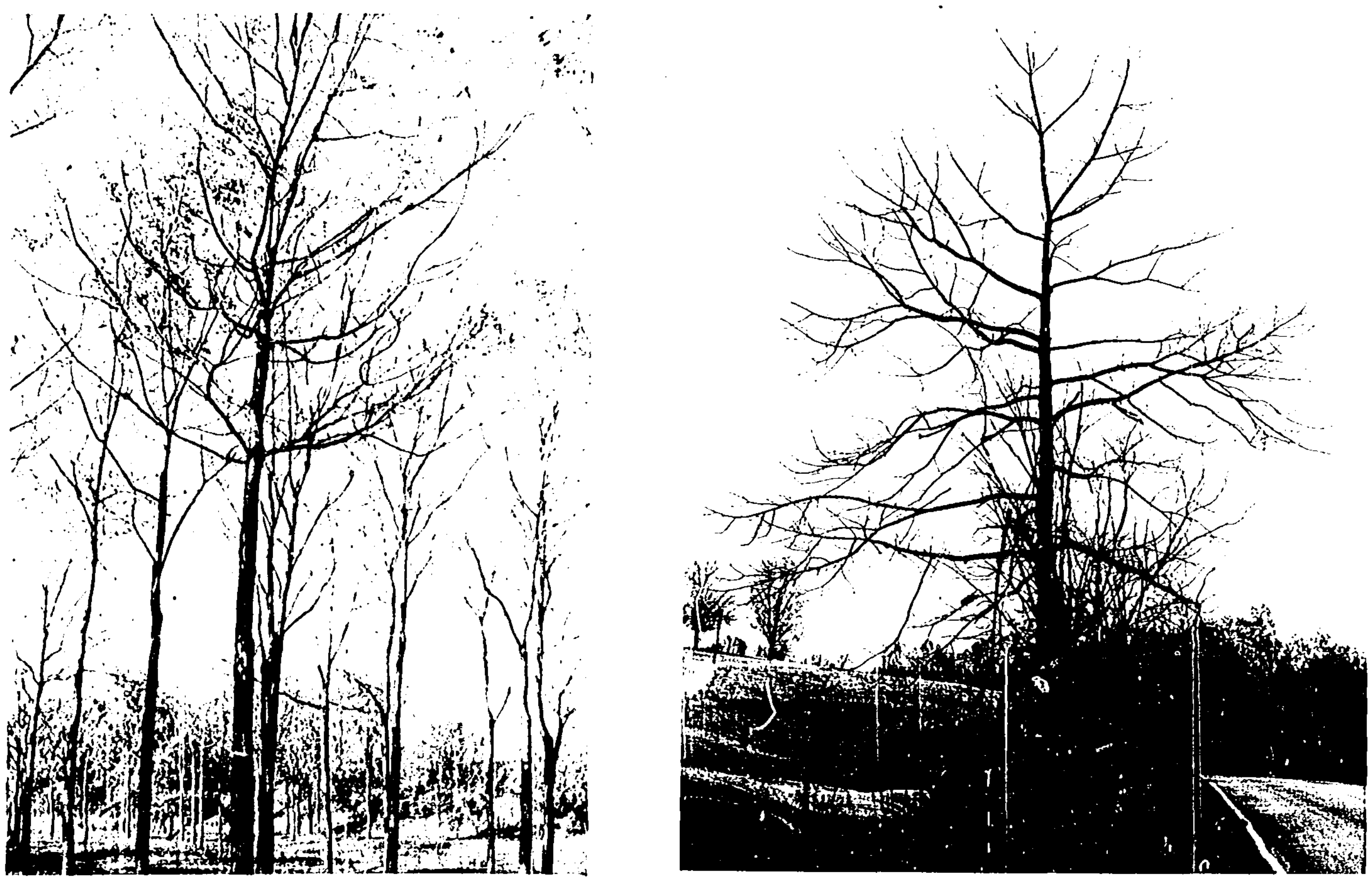

Figure 14. Walnut trees with wide branch angles exhibit an excurrent growth form. Trees like the ones pictured here are quite rare.

partially inhibits the growth of the leaves, and the southern sources have higher apical dominance than the northern sources. This is in opposition to the trend suggested for leaf angle during the first year. An unexplored possibility may explain this contradiction. The southern sources continue to grow in height longer into the fall than the northern sources. It is possible that leaf growth stops before height growth stops. If this is true, the southern sources would have a higher height-leaf length ratio than the northern sources.

Families which varied by 14.3 units were considered different. Only in sources 2 and 3 were there family differences within sources. As would be expected, the majority of the differences between families followed the pattern of the source differences.

No correlations between leaf angle and height-leaf length ratio were run. However, it seems pertinent to point out that family 206 had both the smallest leaf angle and the smallest height-leaf length ratio. Both traits indicate a low degree of apical dominance. Parent tree 206 was considered poor for stem straightness. And on the other extreme, family 602 had both the greatest leaf angle and the greatest height-leaf length ratio. Both traits indicate a high degree of apical dominance. Parent tree 602 was considered average for stem straightness.

General Discussion and Recommendations

Trees with the excurrent type of branching such as the pines, sweet-gum, and yellow-poplar are often said to have strong apical dominance. Trees where the lateral branches grow almost as fast as the terminal shoot giving rise to the decurrent or delinquescent growth habit are said to have weak, or even lack, apical dominance. The oaks, elms, hickories, and maples have these decurrent characteristics (Kozlowski 1964).

Brown et al. (1967) have examined apical dominance in trees from the standpoint of lateral bud inhibition on the current year's growth. Lateral buds on the current year's growth on trees that are characterized by the excurrent form (a cone-shaped crown and a clearly defined bole) normally elongate to varying degrees. Conversely, many of the decurrent or deliquescent species such as the oaks, hickories, and maples exhibit almost complete inhibition of lateral buds on the current year's twigs.

The current interpretations of form in woody plants on the basis of strong or weak apical dominance are basically incorrect, because the patterns of bud inhibition are just the reverse of what they should be according to common usage of the term. Trees with an excurrent form have weak apical dominance, whereas trees with the decurrent form have strong apical dominance. The term "apical control" is suggested to describe the physiological condition governing the excurrent or decurrent pattern of growth. Strong "apical control" could be used to describe the excurrent habit of growth made possible by the initial expression of weak apical dominance or incomplete bud inhibition. Just the opposite would hold true for the decurrent tree forms. Weak "apical control" would describe trees that express strong apical dominance or complete bud inhibition along the currently elongating main leader (Brown et al. 1967).

The conclusions of Brown et al. (1967) appear to "shake" the definition of apical dominance that is presented by Kozlowski (1964). Although some of the differences revolve around the use of the terms "apical dominance" and "apical control", a perplexing unanswered question still remains; "Why do the excurrently formed trees with low degree of apical dominance (Brown et al. definition) generally have wider branch angles and shorter branches?" Brown believes that timing is the important point in what form trees will take. When several lateral buds begin growth almost simultaneously, as they do in the spring in decurrent species, there is a strong negative geotropic response not counteracted by an epinastic control of the terminal bud. As with decapitation during active shoot growth, the lateral buds are tending to grow vertically as did the former main stem, hence narrow branch angles. In excurrent forms, apparently the main stem maintains rigid control over its appendages through a system of delicate balance in growth factors. The precise mechanisms of growth correlations are unknown.[1]

The foregoing discussion has an important bearing on a tree improvement program. On the basis of crown form walnut is classified as a decurrent species. Excurrent forms are rare. For a decurrent species like black walnut we should not expect to find buds on the current season's growth developing into branches. We would say that black walnut as a species has a high degree of apical dominance. As with other traits, we would expect some variation within the species. In 3- to 5-year-old trees, I have observed that some buds on the current season's growth do develop into branches. The hypothesis is advanced that these trees will develop

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[1]Brown, C. L. Department of Botany, University of Georgia, Athens, Georgia. Personal communication in letter concerning apical dominance. 1967.

into more of an excurrent form than trees on which no branches develop on the current season's growth. Whether or not this trait is under strong genetic control is not known. As a rule, in one-year seedlings there is no lateral branch development. Branches normally develop only when the tip is destroyed or damaged. The degree of genetic control in branch development in one-year-old black walnut seedlings is unknown.

As a result of this experimental work, observations and continued review of the literature, the following recommendations seem appropriate:

(1) The technique for measuring epicotyl curvature should be refined, if it is to be used in selection of superior genotypes, families or sources. As used in this experiment, the technique is neither simple, rapid, or practical.

(2) Continue to use leaf angles as an expression of apical dominance. Expand the study so that the range of branch angles in parent trees includes very wide to very narrow.

(3) Continue to use height-leaf length ratio as a measure of apical dominance. For one- and two-year-old seedlings, determine the extent and type of correlation between height growth and leaf extension throughout the growing season.

(4) For walnut trees 3 years old or more, determine the extent of branch development on current season's growth. Conduct a preliminary study in existing plantations and then establish experiments to determine the degree of hereditary control for this trait.

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