GENETIC VARIATION IN JUVENILE CHARACTERS OF

POPULUS DELTOIDES BARTR. FROM THE

SOUTHWESTERN PORTION OF ITS

NATIVE RANGE

By

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PREFACE

This study is an effort to document the genetic variation and genetic parameters of juvenile characters in the eastern cottonwood (<u>Populus deltoides</u> Bartr.) population of the southern Great Plains, and to preserve eastern cottonwood germplasm of this region for future genetics and breeding research. Funds for this work were made available in part by a grant from the United States Forest Service, Southern Forest Experiment Station and in part by McIntire-Stennis, Oklahoma Agricultural Experiment Station.

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CHAPTER I

INTRODUCTION

Eastern cottonwood (Populus deltoides Bartr.) is an important and valuable forest tree species of the central and eastern United States (Figure 1). Cottonwood is a principal component of the bottomland forests throughout this region. It is a pioneer (or early successional) species, being shade intolerant and fast growing. Seasonal flooding of natural watercourses provides cottonwood with naturally prepared, alluvial seed beds. Prolific seed production, timely seed dispersal and rapid seed germination following the receding flood waters allows cottonwood the opportunity to form in its characteristic pure and even-aged stands. Occasionally, cottonwood may be found in open mixtures associated with the following species: green ash (Fraxinus pennsylvanica Marsh.), white ash (F. americana L.), sugarberry (Celtis laevigata Marsh.), hackberry (C. occidentalis L.), slippery elm (<u>Ulmus</u> rubra Muhl.), American elm (<u>U</u>. americana L.), black willow (Salix nigra Marsh.), river birch (Betula nigra L.), American hornbeam (Ostrya virginiana (Mill.) K. Koch), sycamore (Platanus occidentalis L.), black tupelo (Nyssa sylvatica Marsh.) and boxelder (Acer negundo L.) (Fowells, 1965).

Eastern cottonwood is native throughout the state of Oklahoma and the eastern half of Texas (Figure 1). Some authors (Fowells, 1965; Little, 1981) distinguish between two varieties within the southern



Figure 1. Native Range of Eastern Cottonwood (Populus deltoides Bartr.)

Great Plains region--eastern (<u>Populus deltoides</u> Bartr. var. <u>deltoides</u>) and plains (<u>P</u>. <u>deltoides</u> var. <u>occidentalis</u> Rydb.). Other authors (Brockman, 1968; Preston, 1976) classify plains cottonwood as a unique species (<u>Populus sargentii</u> Dode.). Plains cottonwood is distinguished as having smaller, often broader than long and more closely toothed leaves than eastern cottonwood (Little, 1981). In addition, plains cottonwood is usually slower growing and smaller in stature at maturity than eastern cottonwood. Natural hybridization between the two varieties occurs frequently in the central one-third (overlapping region of Figure 2) of Oklahoma. Hybrids are usually intermediate (when compared to their parents) in their phenotypic expression of leaf and growth characters.

The value of eastern cottonwood can be characterized in three ways. First, cottonwood is a source of valuable raw material. Many finished and unfinished forest products utilize cottonwood wood, fiber and/or foliage as raw material, including the following products: crates, boxes, pallets, plywood corestock, lumber, pulp, flakeboard particles, excelsior, mulch, insulation, fuelwood and animal feed supplement (Barger and Ffolliot, 1971; Crist et al., 1979).

Second, eastern cottonwood is a desirable reforestation species. The demand for wood and fiber has interested forest industries and small landowners in establishing intensive culture, short rotation, biomass plantations. Cottonwood, being easily propagated and fast growing, is an excellent choice for such plantings (Mohn, 1973). Cottonwood is also a good species for use in soil stabilization projects and shelterbelt plantings (Lovett, 1979).



Figure 2. Native Ranges of Eastern Cottonwood Variety Eastern (<u>Populus</u> <u>deltoides</u> Bartr. var. <u>deltoides</u>) and Eastern Cottonwood Variety Plains (<u>P. deltoides</u> var. <u>occidentalis</u> Rydb.) in Oklahoma and Texas

Third, eastern cottonwood is a widely used and an extremely useful species in forest tree genetics research (Pauley, 1949; Muhle Larson 1970; Schreiner, 1970). Applied research leading to genetically improved cottonwood strains is directly related to improving the quality of raw material and the potential yield of reforestation stock (Johnson, 1972). The potentially large amount of genetic variation (due in part to a large native range), relative ease of vegetative propagation and control crossing, early flowering, and short rotation and generation length (due to fast growth and early sexual maturity) lend cottonwood to genetic improvement. In addition, research opportunities in interspecific hybridization, tissue culture, recombinant DNA and other cytogenetic techniques have and will lead to applied genetic gains in eastern cottonwood and an increase in the basic knowledge of forest tree genetics.

From an applied research viewpoint, genetic improvement of eastern cottonwood is a must if cottonowood is to be cultured for biomass production, soil stabilization or shelterbelts in Oklahoma, Texas and surrounding areas. The high costs of intensive culturing will not be recovered if genetically inferior or ill-adapted planting stock is utilized. Improved cottonwood strains and genetically superior clones have been developed and identified in the Mississippi River Valley and other areas east of Oklahoma and Texas (Muhle Larson, 1970; Maisenhelder, 1970; Schreiner, 1970; Randall, 1973); however, these stocks are likely to be poorly adapted to Oklahoma and Texas growing conditions (Jokela et al., 1982). Dependence on natural regeneration or unimproved

planting stock results in undesirable stocking, slow growth and poor wood and fiber quality. A tree improvement program that would develop a group (strain) of high quality, rapid growing eastern cottonwood clones will provide Oklahoma and Texas landowners with a tree planting incentive, by guaranteeing an adequate supply of genetically improved planting stock.

The major questions that need to be answered before any genetic improvement program can begin is how much and what types of genetic variation are available in the source population? Without genetic variation, conventional tree breeding techniques will be futile. Without information on the type of variation (i.e. among geographic source, among families, within families, genotype by environment interaction, etc.) or pattern (i.e. clinal or ecotypic) the optimal breeding method is unknown.

Eastern cottonwood improvement efforts in the Mississippi River Valley have emphasized clonal selection and testing (Farmer, 1966; Farmer and Wilcox, 1968; Mohn and Randall, 1969 and 1971; Jokela et al., 1982; Randall and Cooper, 1973). This method is effective in identifying superior genotypes and allows for their indefinite propagation. However, only naturally existing genotypes are tested. No opportunity for new, recombined genotypes is possible. In a population improvement approach, selection, breeding and testing are utilized to produce new and improved genetic combinations. At any stage in the program the improved genotypes may be recommended and released as vegetative propagules for commercial use. With the population

improvement breeding method, selections may be based on stand or family mean performance as well as the individual's performance. The selected individuals may then be intercrossed to produce the next generation from which new selections may be made. As a result of selection and intercrossing, original gene frequencies are changed which in turn results in new genotypes and genotypic frequencies in the new, "improved" population. The gradual gene and genotypic frequency changes and maintenance of genetic variability are the basis of recurrent selection and population improvement (Stonecypher, 1969).

In an effort to initiate an eastern cottonwood population improvement program for Oklahoma and Texas, this study will attempt to answer the basic questions of how much genetic variation and what types exist in the source population. The source population consists of the native eastern cottonwood (eastern and plains variety) in the southwestern portion of its range. This area includes the following states and areas of states: Oklahoma, Texas, southeast Colorado, south Kansas and west Arkansas.

Many genetic studies have been conducted in order to answer these questions, but they have not dealt with the southwestern eastern cottonwood population and Oklahoma planting environments (Jokela, 1964; Wilcox and Farmer, 1967; Rockwood, 1968; Farmer, 1970b; Mohn and Randall, 1971; Eldridge et al., 1972; Ying, 1974; Jokela and Mohn, 1976; Friend, 1981). This genetic variation study is designed to test the native eastern cottonwood population of the southern

Great Plains under nursery conditions of central and eastern Oklahoma. In addition, the nursery tested trees will be preserved in field plantings for further research and breeding activites.

Specifically, the objectives of this study are to answer the following questions: (1) How much genetic variation in juvenile characters exists among native stands and among open-pollinated families of eastern cottonwood in the southwestern portion of its range?, (2) Do genotype by environment interactions exist and if so, what type are they? and (3) What pattern of the genetic variation can be described or delineated? In addition, narrow sense heritability of each juvenile character and genetic correlation coefficients between some characters will be estimated.

CHAPTER II

LITERATURE REVIEW

In the past 25 to 30 years many eastern cottonwood provenance and progeny tests have been conducted and reported (Pauley and Perry, 1954; Wilcox and Farmer, 1967; Rockwood, 1968; Mohn and Pauley, 1969; Farmer, 1970b; Mohn and Randall, 1971; Eldridge et al., 1972; Jokela and Mohn, 1976; Ying and Bagley, 1976a; Friend, 1981). These results have been useful in identifying good seed sources, describing patterns of genetic variation, establishing estimates of various population genetic parameters and preserving germplasm for future breeding and genetics research. The genetic parameters--genetic variation and heritability of traits and genetic correlations between traits -- form the basis from which a tree improvement program must operate. Future breeding strategy and economic justification of the improvement program are contingent upon accurate estimates of population genetic parameters. However, the fact remains that no attempt has been made to survey, document and preserve the genetic variation among and within native stands of eastern cottonwood of the southwestern portion of its range. This region contains many good cottonwood sites with long growing seasons, and it is in need of genetically improved planting stock for future tree planting operations (Walker, 1967).

Posey et al. (1969) sampled the phenotypic variation of three characters in a portion of the southern Great Plains eastern cotton-

wood population. Twenty-four stands (plots) were systematically chosen along three major rivers in Oklahoma. Specific gravity, fiber length and radial growth rate measurements were made on ten trees per stand.

Results indicate that specific gravity increases from east to west along rivers (Posey et al., 1969). Significant differences in specific gravity were due to among stands and among trees-withinstands. Fiber length decreased from east to west and sifnificant differences occurred among rivers (north-south trend). These differences are a combination of genetic and environmental effects.

Posey (1969) also collected vegetative cuttings from the sampled trees and rooted these cuttings in the Oklahoma Division of Forestry's nursery near Norman, Oklahoma. Height, diameter at 20 inches, number of limbs per foot, specific gravity and fiber length were measured or calculated after one growing season. Stand means for specific gravity and number of limbs per foot increased from east to west, with no significant differences among rivers. Fiber length, diameter and height stand means decreased from east to west. A 30 percent difference in height between tallest and shortest stand means and a 110 percent difference in height between tallest and shortest clone means were found. These results indicate that a very definite pattern of genotypic variation is present in the Oklahoma population of eastern cottonwood. However, no information about additive and non-additive genetic variation or genotype by environment interactions was extracted.

Farmer and Wilcox (1965) analyzed genetic variation in juvenile characters of half-sib eastern cottonwood families. Seed was collected from 25 selected female trees of Mississippi origin. The halfsib progenies were grown for two years, after being cut back following the first growing season. Height and diameter were measured before being cut back and height, diameter, specific gravity and fiber length were measured following the third (overall) year. Significant differences (.01 probability level) among families were found for both first and third year height. No significant differences among families were found for first or third year diameter, third year specific gravity or third year fiber length. These results indicate that genetic variation is available for juvenile height in the sampled population, but not for diameter, specific gravity or fiber length.

Farmer and Wilcox (1965) found very high narrow sense heritability (h^2) estimates for first year height and diameter, .93 and .56, respectively. Third year characters showed lower heritability estimates--height, $h^2 = .35$; diameter, $h^2 = .16$; specific gravity, $h^2 = .62$; and fiber length, $h^2 = .40$. A negative, but non-significant genetic correlation (r_G) was found between third year diameter and specific gravity $(r_G = -.07)$, while a positive and significant genetic correlation was found between third year diameter and fiber length

Farmer (1970b) reported results of an open-pollinated progeny test conducted in Mississippi. Seed was collected from 81 trees in

natural stands; 29 trees were phenotypically selected and 52 trees were chosen at random. The seeds were planted in early August, and in late August the seedlings were transplanted into a nursery in a balanced nine by nine lattice square experimental design with ten replicates. In February the seedlings were outplanted, with design intact, into a field location.

Measurements were taken following the first and second field growing seasons. Variation among open-pollinated families was significant (.05 proability level) for all measured characters--first and second year height, second year diameter at one foot, first year incidence of Melampsora leaf rust (Melampsora spp.), second and third year date of foliation, specific gravity and fiber length. Mean height and diameter of progeny of phenotypically selected parents and randomly chosen parents were not significantly different and ranges of family means were similar. Farmer (1970b) found that 5.9 to 12.8 percent of the total variation was due to among family variation for height and diameter, while 51 to 91.6 percent was due to among family variation for leaf rust incidence and foliation date. Farmer (1970b) implied that mass selection would appear to be very effective for improving leaf rust resistance and foliation date, and less effective for improving growth traits (i.e. height and diameter). Genetic correlation of specific gravity with growth rate was found to be too low to be of practical importance (Farmer, 1970b).

Friend (1981) conducted and reported results of a limited-range eastern cottonwood provenance and open-pollinated progeny test. Seed

was collected from six trees per stand, from two stands per geographic source and from 15 sources in the southern United States. The seed was planted in pots in a shade house and following germination each pot was thinned to one plant. The pots were transferred outside for two weeks to allow the seedlings the opportunity to acclimate to the outdoor conditions before transplanting.

Three of the six open-pollinated families per stand were selected for nursery testing, based on percent survival through the shade house and acclimation period. This reduced the size of the experiment in half (i.e. 180 families to 90 families). The selected families were transplanted into two nurseries at environmentally diverse Mississippi locations--Starkville and Stoneville. A randomized complete block design with four replicates per location and four tree family-rowplots by source was utilized, with plots randomized within each sourceblock. Irrigation and weed control were provided, when necessary, throughout the two year nursery study. Fertilizer was applied to both plantings in September of the first year and in June of the second year. All data were collected during the second growing season, including the following characters: date of budbreak, date of foliation, height (throughout the season), root collar diameter (throughout the season), leaf dimensions and weight and Melampsora leaf rust incidence.

Friend (1981) utilized the analysis of variance procedure and F-tests (.05 probability level) to test the effects of planting site,

seed source, stand within-seed source and family-within-standwithin-seed source. Duncan's New Multiple Range Test was used to aid in determining patterns of variation among geographic sources. Variance components were estimated by equating observed with expected mean squares from the analysis of variance output. Analysis of covariance was used to determine phenotypic and genetic correlations between characters, using phenotypic and family covariances with their corresponding variances.

Variation among sources was significant for the first half of the growing season for diameter and throughout the season for height. All other genetic sources of variation (stand and family) and genotype by environment interactions were not significant for diameter. Among family variation was significant for height through the first half of the season, while among stand variation and all genotype by environment interactions were not significant (Friend, 1981).

Friend (1981) found significant genetic variation (among sources, stands and families) for date of budbreak and date of foliation. Among family variation across all seed sources accounted for 80 percent of the total phenotypic variation for date of budbreak and 78 percent for date of foliation. All genotype by environment interactions for dates of budbreak and foliation were not significant. Friend (1981) noted, in general, that southern sources broke bud and foliated earlier than northern sources, and western sources broke bud and foliated earlier than eastern sources (excluding sources east of the Appalacian Mountains).

Friend (1981) reported Melampsora leaf rust incidence to be near normally distributed. A visual scoring system (from zero to six) was used to rate each individual. A zero score meant no uredia present and a six count indicated numerous crinkled leaves with some defoliation. Variation among sources and among families-withinstands-within-sources was significant for leaf rust score. Variation among families across all seed sources accounted for 69 percent of the total phenotypic variation. In general, southern latitude sources were more rust resistant than middle and northern latitude sources.

Friend (1981) calculated the following between trait genetic correlation coefficients (r_G) : final height with final diameter, $r_G = .68$; final height with leaf rust incidence score, $r_G = -.41$; and final diameter with leaf rust incidence score, $r_G = -.26$. The following phenotypic correlation coefficients (r_P) based on family means within-sources were also calculated: final height with final diameter, $r_P = .84$; final height with leaf rust incidence score, $r_P =$ -.36; and final diameter with leaf rust incidence score, $r_P = -.36$; and final diameter are strongly and positively correlated and height and diameter are adversely affected by severe rust infections (Friend, 1981).

Jokela and Mohn (1976) reported the results of a range-wide eastern cottonwood seed source study. Seed was collected from 243 parent trees in 17 states. Mortality of northern seedlots was high in southern plantings, as was the mortality of southern seedlots in

northern plantings. Date of leaf flush showed no clear geographic pattern of variation, with the possibility that northern and western sources flushed somewhat earlier than southern and eastern sources. Winter injury observations indicated that the further north a seedlot is moved the more severe the injury will be. Southern sources exhibited greater growth rate, apparently due to their tendency to continue growing later in the fall than northern sources. However, excessive northward movement of sources resulted in poor growth rate (Jokela and Mohn, 1976).

Jokela and Mohn (1976) found Melmapsora leaf rust incidence to be more severe on northern sources than on southern sources. As an example, in the central Illinois planting, trees originating from Minnesota, Missouri and Illinois were more severely infected than trees from Louisiana and Mississippi. Theilges and Adams (1975) found a similar north-south trend of Melampsora leaf rust resistance in a study of eastern cottonwood of the Ohio River Valley Region. Jokela and Mohn (1976) state

the varying incidence of leaf rust . . . appears to be due largely to an interaction between seed origin and location of planting and may be related to senescence and other physiological phenomena influenced by climate rather than by biotype of the rust (p. 121).

Evidence to support this statement comes from the close relationship between incidence of rust during the growing season and latitude and longitude of seed origin.

Dhir (1974) and Ying (1974) reported that east-west variation is more important than north-south variation in eastern cottonwood;

however, southern sources were under-represented in both of their studies and the pattern of variation is dependent upon the population sampled.

After reviewing much eastern cottonwood research, Jokela and Mohn (1976) concluded that extreme eastern and western sources and other limited segments (along specific river systems) of eastern cottonwood's range need more detailed study.

The southern Great Plains region of the United States lies at the extreme western and southern edge of eastern cottonwood's native range. Most river systems of this area flow from west to east and are adjacent to excellent sites for cottonwood growth. This combination makes the Oklahoma and Texas eastern cottonwood population ideal for detailed genetic variation study. The region's climatic and physiographic characteristics are much different than that of the Mississippi and Ohio River Valleys and the upper Midwest; thus, information about genetic variation in the southern Great Plains' eastern cottonwood population is needed (Posey et al., 1969). This information will give an Oklahoma and Texas eastern cottonwood improvement program a basis from which to make future selection and breeding methodology decisions. In addition, the preserved eastern cottonwood germplasm resulting from this study will be available for future genetics and breeding research.

CHAPTER III

MATERIALS AND METHODS

Seed Collection and Handling

In June of 1982 open-pollinated eastern cottonwood seed was collected from five mother trees in each of 40 natural stands within the southwestern portion of eastern cottonwood's native range (Figure 3 and Table XXV, Appendix A). A total of 197 open-pollinated families (seedlots) were collected. The stands were systematically located along the major river systems which traverse this area, and were assumed to be random members of the population of stands in the area. Distances between stands were maintained at approximately 100 miles. Within a stand, parent tree choice was at random except when mature seed was limiting. In these cases only trees with an adequate amount of mature seed (25 to 50 catkins) were chosen as seed trees. Spacing between seed trees within-stands was maintained at a 200 foot minimum, to minimize relatedness of parent trees and/or collected progenies.

Following seed collection, the catkins were placed loosely in paper bags which were suspended from wire. This allowed for rapid air drying of the seed without exposure to excessive heat. After a few days of drying, the catkins were processed with a blender-vacuum apparatus in order to separate the catkins and "cotton" from the seed.



Figure 3. Location of Seed Collection Stands

Catkins of individual open-pollinated families were placed on a suspended screen in the lower portion of the blender pitcher. A vacuum hose was inserted into the top of the blender through the lid. The spinning blender blades caused the seed to be separated from the impurities and the vacuum sucked the "cotton" and the lighter impurities out the top, while the heavier seed filtered through the screen to the base of the blender pitcher. Upon drying and cleaning, the seed was refrigerated at 4°C until planting.

After the drying and cleaning process, 50 seed per openpollinated family were germination tested to estimate family germination percentage. The seeds were placed on damp chempack covered germination trays and placed in a germinator, with day time air temperature controlled at 27°C and night time air temperature at 18°C. Seedlots that failed to germinate or showed poor germination (less than 20 percent) were replaced with new seedlot collections. The new collections were made from different seed trees in the same stand. A total of 62 seedlots were recollected because of poor germination. Based on percent germination, the highest four families per stand were selected for use in the greenhouse and nursery phases of this study.

Greenhouse Phase

On July 7 to 9, 1982, 15 seeds from each of four parent trees of each stand (three parent trees from stand 41) were planted in

5.1 cm by 5.1 cm by 12.7 cm deep (2 inch by 2 inch by 5 inch) containers (pots) in the Oklahoma State University Department of Forestry's greenhouse in Stillwater, Oklahoma. Table XXVIII, Appendix B lists the families-within-stands (and their percent germination) that were planted in the greenhouse. A sterilized peat-sand soil mixture was used as a potting medium.

The pots were pre-arranged (before planting) in a randomized complete block experimental design with ten replicates and six pot (tree) family-row-plots. A heirarchal classification scheme was utilized with parent trees (open-pollinated families) nested in stands. A total of 159 open-pollinated families were selected and planted in the greenhouse phase (i.e. four families from 39 stands and three families from stand 41).

Following seedling emergence, each pot was thinned to three plants and eventually to one plant after three to four weeks of growth. This thinning was at random with the exception of moderate selection for seedling vigor. All pots were watered with a complete (macro and micro) fertilizer solution from below on a daily schedule. Day length was maintained at 17 hours.

Following the sixth week of growth, half of the experiment (five replicates) was moved into a wood lathe shade house to allow the seedlings to acclimate to outdoor conditions before outplanting. While in the shade house, the watering schedule continued as in the greenhouse. These seedlings remained in the shade house for a period of 14 days. After the seventh week of growth, the other five repli-

cates were moved into the shade house for acclimatization. These seedlings also continued to receive daily watering and remained in the shade house for an 11 day period.

Nursery Phase

Immediately following shade house acclimatization, the seedlings were outplanted at two diverse nursery environments -- Oklahoma Division of Forestry's nursery (Norman nursery) south of Norman, Oklahoma and Oklahoma State University's temporary nursery (Broken Bow nursery) southeast of Broken Bow, Oklahoma (Figure 4 and Table XXVII, Appendix A). The five replicates that were removed first from the greenhouse and received the 14 day shade house treatment were planted at the Norman nursery on August 31 to September 2, 1982. The five replicates that received the 11 day shade house treatment were planted at the Broken Bow nursery on September 7 and 8, 1982. The experimental design of the study was a randomized complete block with two locations and five replicates per location. Family-plot size was reduced from six trees to four trees because of seedling mortality, while replicate identities were maintained. The nursery locations were assumed to be a random sample of two locations from the population of nursery locations within central and eastern Oklahoma.

One border row of extra seedlings was planted around each planting to assure equal tree-to-tree competition for all study trees. Between tree spacing at each site was 45.7 cm (18 inches) within rows and



Figure 4. Location of the Norman and Broken Bow Nurseries

99.1 cm (39 inches) among rows. Replicates, as well as plots, were oriented in rows at both locations.

A total of 3,109 seedlings (excluding border trees) were planted at Norman, while 3,153 seedlings (excluding border trees) were planted at Broken Bow. At the time of nursery planting, the Norman and Broken Bow sites had 44 and 15 family-plots, respectively, with fewer than four trees. All 159 open-pollinated families of the greenhouse phase were represented in each replicate of the nursery phase.

Both nursery sites were thoroughly tilled and disked immediately before planting. Air temperatures at planting time reached daily maximums of 38°C and 35°C at Norman and Broken Bow, respectively. To alleviate the problems associated with the extreme heat, both sites were irrigated several times daily during planting operations. Irrigation was continued (when necessary) at both nurseries for one month, to facilitate seedling establishment. Above ground sprinkler irrigation systems were utilized at both nursery sites.

The nursery phase of this study culminated following the 1983 growing season. During the period following seedling establishment, complete weed control was maintained in the Norman nursery planting, while only partial control was accomplished in the Broken Bow planting. Machine cultivation and hand hoeing were the principal modes of weed control at both sites.

Measurements

The following data were collected for each seedling at both nursery locations:

Variable Name

Measurement

Date of Leaf Fall 1982 (LF1)
Height 1982 (HT1)
Date of Leaf Fall 1983 (LF2)
Melampsora Leaf Rust Score 1983 (MLR)
Survival 1983 (SURV)
Height 1983 (HT2)
Diameter 1983 (DIA)
Number of Branches 1983 (BR)

first year date of leaf fall first year height second year date of leaf fall second year rust score second year (dead or alive) second year height second year diameter second year number of branches

In addition, the height of each seedling was measured at the conclusion of the greenhouse phase (GHT) on August 24, 1982.

Greenhouse height (GHT) was measured from the surface of the potting soil medium to the apex of the tallest growing point. It was measured with a metric ruler to the nearest tenth (.10) cm. Height 1982 and height 1983 (HT1 and HT2) were measured in December of 1982 and 1983, respectively, at both locations. The measurements were made from the soil surface to the tallest terminal bud. A meter stick was utilized to measure height 1982 to the nearest tenth (.10) cm. Height 1983 measurements were made with a 24 foot (7.3 m) collapsable measuring pole. These data were recorded in feet and inches and later
converted to centimeters. Survival 1983 was recorded as dead or alive--alive if a height 1983 measurement could be made--and converted to percent living trees per family-plot.

Date of leaf fall 1982 and date of leaf fall 1983 (LF1 and LF2) were recorded as the number of days past November 1, 1982 for LF1 and October 31, 1983 for LF2, when one or zero leaves remained on the individual tree. Both nursery plantings were examined for date of leaf fall 1982 and 1983 twice weekly, through January 11, 1983 for LF1 and December 20, 1983 for LF2.

Diameter 1983 (DIA) was measured on the main stem of each tree at 12 inches (30.5 cm) above the soil surface, during December of 1983. A machinist type caliper was used to make the measurements to the nearest one-thousandth (0.001) inch (.25 mm). These data were later converted to millimeters.

Melampsora leaf rust score 1983 (MLR) was observed and recorded on October 4 and October 10, 1983 for the Norman planting and on October 15, 1983 for the Broken Bow planting. The Melampsora leaf rust score reflects the percentage of the individual tree's total leaf surface area that was covered with <u>Melampsora</u> spp. urediospores on the date(s) of observation. Table I lists the Melampsora leaf rust scores that were used to indicate the approximate percentage of upper leaf surface area that was infected at the time of observation.

Number of branches 1983 (BR) was counted and recorded during December of 1983. A branch was considered to be any limb that could be traced directly back to the main stem (leader). The variable number of branches per decimeter 1983 (BRPD) was calculated using number of branches 1983 and height 1983 data.

TABLE I

MLR	Score	Approximate % of Upper Leaf Surface Area Covered by Urediospores						
	0	less than 10						
	20	greater than 10 but less than 30						
	40	greater than 30 but less than 50						
	60	greater than 50 but less than 70						
	80	greater than 70 but less than 90						
]	00	greater than 90						

MELAMPSORA LEAF RUST SCORES AND SCORING CRITERION

Data Analysis

Means

The MEANS procedure of the Statistical Analysis System (SAS, 1982a), was utilized to compute greenhouse, nursery, stand and family-withinstand means and standard errors of the means for all measured or observed characters.

Variation Analysis

<u>Frequency Histograms</u>. The SAS (1982a) procedure CHART was used to construct frequency histograms of family-plot means for each nursery character at each location, over both locations and for greenhouse height. These histograms were used for acquiring a general feel towards the range and distribution of these data.

Analysis of Variance and F-Tests. The VARCOMP procedure of SAS (1982b) was utilized to compute Type I sums of squares and mean squares for each factor of the experimental design models (Figure 5). All factors in both models were assumed to be random. Replicate-withinlocation by stand and by family-within-stand interactions were assumed to be negligible and therefore included in the error. Table II contains the format of the greenhouse and separate nursery location analysis of variance procedure and the F-tests in terms of the expected mean squares. The combined location analysis of variance format and F-tests are shown in Table III. F-tests were constructed in accordance with the expected mean squares to test the hypothesis of equal means among the different levels of the factors (Steel and Torrie, 1980). F-values were calculated by equating the computed (observed) mean squares with the expected mean squares. Calculated F-values were declared statistically significant if the probability of obtaining a larger F-value by chance was .05 or less. For each nursery character an analysis of

Greenhouse and Single Nursery Location Model

 $Y_{jkl} = M + R_{j} + S_{k} + F_{l(k)} + E_{jl(k)}$ Note: $Y_{jkl} = mean of the 1th family within the kth stand$ of the jth replicate<math display="block">M = single location or greenhouse mean $R_{j} = effect of replicate j$ $S_{k} = effect of stand k$ $F_{l(k)} = effect of family 1 within stand k$ $E_{jl(k)} = error (among plot)$

Pooled Locations Model

$$\begin{split} Y_{ijkl} &= M + L_i + R_j(i) + S_k + LS_{ik} + F_{1(k)} + LF_{il(k)} + E_j(i)l(k) \\ \text{Note: } Y_{ijkl} &= \text{mean of the lth family within the kth stand} \\ &M &= \text{pooled locations mean} \\ &L_i &= \text{effect of location i} \\ &R_j(i) &= \text{effect of replicate j at location i} \\ &S_k &= \text{effect of stand k} \\ &LS_{ik} &= \text{effect of location i by stand k interaction} \\ &F_{1(k)} &= \text{effect of family l within stand k} \\ &LF_{il(k)} &= \text{effect of location i by family l within} \\ &E_{i(i)l(k)} &= \text{error (among plot)} \end{split}$$

Figure 5. Experimental Design Models for Single and Pooled Locations

TABLE II

FORMAT OF GREENHOUSE AND SINGLE NURSERY LOCATION ANALYSIS OF VARIANCE AND F-TESTS

Source of Variation *	Degrees of Freedom	Mean Square	e Expected Mean Square
Replicate	9 or 4		
Stand	39	MS ₃	$V_{E} + cV_{F(S)} + cV_{S}$
Family (Stand)	119	MS ₂	$V_{E} + cV_{F(S)}$
Error	**	MS_1	v _E
<u>F-Tests:</u> ^F Stand ^F Famil	$H = \frac{MS_3}{MS_2}$	with 39 and 1 $d = \frac{MS_2}{MS_1}$	119 degrees of freedom with 119 and error** degrees of freedom

Note: $V_{\rm F}$ = variance among (family) plot means

 $V_{F(S)}$ = family-within-stand variance component

- V_{s} = stand variance component
- c = coefficient in expected mean square as computed by the SAS (1982b) procedure VARCOMP
- * all effects considered random
- ** The error degrees of freedom at each location varies, depending on the character being analyzed. Tables IV, V, VII, IX, XI, XIII, XV, XVII and XIX contain the appropriate error degrees of freedom.

TABLE III

FORMAT OF POOLED NURSERY LOCATIONS ANALYSIS OF VARIANCE AND F-TESTS

Source of Variation *	Degrees of Freedom	Mean Squa	re Expected Mean Square
Location	1		
Replicate (Location)	8		
Stand	39	MS ₅	$V_{E} + cV_{L \cdot F(S)} + cV_{F(S)} +$
			$cV_{L \cdot S} + cV_{S}$
Location X Stand	39	MS ₄	$V_{E} + cV_{L \cdot F(S)} + cV_{L \cdot S}$
Family (Stand)	119	MS 3	$V_{E} + cV_{L \cdot F(S)} + cV_{F(S)}$
Location X Family (Stand)	119	ms ₂	$V_{E} + cV_{L} \cdot F(S)$
Error	**	MS ₁	v _E
<u>F-Tests:</u> ^F Stan	$d = \frac{MS_{5} + MS}{MS_{4} + MS}$ $\frac{(MS_{4} + MS_{4})^{2}}{(MS_{4})^{2} + (MS_{4})^{2} + (MS_{$	$\frac{2}{\text{with}}$ with $\frac{(\text{MS}_3)^2}{(\text{MS}_3)^2}$ 119	$\frac{(MS_5 + MS_2)^2}{\frac{(MS_5)^2}{39} + \frac{(MS_2)^2}{119}}$ and degrees of freedom (Cochran and Cox, 1957)
FLoca	tion X Stand	$=\frac{MS_4}{MS_2}$	with 39 and 119 degrees of freedom
^F Fami	ly (Stand) =	MS ₃ MS ₂ f	ith 119 and 119 degrees of reedom

<u>F-Test</u> F	<u>s (Continued):</u> Location X Family (Stand) = $\frac{MS_2}{MS_1}$ with 119 and error** degrees of freedom
Note:	V_{E} = variance among (family) plot means
	V L·F(S) = location by family-within-stand interaction variance component
	$V_{F(S)}$ = family-within-stand variance component
	$V_{L \cdot S}$ = location by stand interaction variance component
	V_{S} = stand variance component
	<pre>c = coefficient in expected mean square as computed by the SAS (1982b) procedure VARCOMP</pre>
	* all effects considered random
	** The error degrees of freedom varies, depending on the character being analyzed. Tables VI, VIII, X, XII, XIV, XVI, XVIII and XX contain the appropriate error degrees of freedom.

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variance and F-tests were computed on separate location data and pooled location data, using plot (family) means as the individual observations. Analysis of variance and F-tests were also computed for greenhouse height. The use of plot means eliminated the need for estimating the within-plot mean square.

Simple Correlation of Stand Means with Stand

Origin Data

Pearson correlation coefficients were calculated for each character using pooled (both locations) stand means and each of the following stand origin variables: latitude (°North), longitude (°West), number of frost free days, mean annual precipitation (cm), elevation (m above sea level), mean annual minimum temperature (°C) and mean annual maximum temperature (°C). Tables XXV and XXVI, Appendix A present the stand origin data. The Pearson correlation coefficient (r) between two variables (X and Y) is represented by the following exression:

$$r_{XY} = \frac{COV_{XY}}{[s_X^2 \cdot s_Y^2]^{\frac{1}{2}}}$$
(SAS, 1982a), (1)

where COV_{XY} = covariance of variable X and variable Y, s_X^2 = variance of variable X and s_y^2 = variance of variable Y.

In this equation, X represents the stand means for a specified character and Y represents the data of a specific stand origin variable (e.g. HT2 and mean annual precipitation). These correlation coefficients can be useful information in attempting to delineate or explain geographical or environmental patterns of (among stand) variation (e.g. trees originating from higher elevations may tend to drop their leaves earlier), especially if significant differences among stand means exist. The SAS (1982a) procedure CORR was utilized to compute these correlation coefficients and their significance.

Variance Component and Heritability Estimation

Family-within-stand mean narrow sense heritability estimates (h²) were calculated using variance components. Heritability was estimated for each character, using separate nursery location data, greenhouse height data and combined location data (Figure 6). Variance components were estimated by equating observed mean squares, from the analysis of variance, with expected mean squares (Tables II and III). Standard errors for each heritability estimate were calculated. Figure 26, Appendix D presents the formula utilized in computing the standard errors of the heritability estimates.

Stand and family-within-stand components of variance were also estimated in terms of percent of the total phenotypic variation (single and pooled locations) among family-plot means. These variance components as a percentage of the total phenotypic variation can be directly compared across characters; thus revealing an indication of

Single Nursery Location and Greenhouse

$$h^{2} = \frac{\nabla_{F(S)}}{\frac{\nabla_{E}}{i} + \nabla_{F(S)}}$$

Note: V_E = variance among (family) plot means $V_{F(S)}$ = family-within-stand variance component i = coefficient associated with $V_{F(S)}$ of MS₂ (Table II)

Pooled Nursery Locations

$$h^{2} = \frac{V_{F(S)}}{\frac{V_{E}}{j} + \frac{V_{L} \cdot F(S)}{k} + V_{F(S)}}$$

Note: $V_{L \cdot F(S)}$ = location by family-within-stand interaction variance component

j = coefficient associated with V_{F(S)} of MS₃ (Table III)
k = j / coefficient associated with V_{L·F(S)} of MS₃
(Table III)

Figure 6. Formulae for Heritability Estimates

the relative importance of stand versus family-within-stand variation for each character. The following equation was used for calculating the estimated total phenotypic variance among family-plot means at a single location:

$$V_{P_1} = V_S + V_{F(S)} + V_E$$
, (2)

where V_{P_1} = total phenotypic variance (single location) among family-plot means, V_S = stand variance component, $V_{F(S)}$ = family-within-stand variance component and V_E = variance among family-plot means.

The total phenotypic variance among family-plot means over both locations was estimated using the following equation:

$$V_{P_2} = V_S + V_{L^*S} + V_{F(S)} + V_{L^*F(S)} + V_E$$
, (3)

where V_p = total phenotypic variance (pooled locations) among 2 family-plot means,

 $V_{L^{*}S}$ = location by stand interaction variance component and $V_{L^{*}F(S)}$ = location by family-within-stand variance component.

Genetic Correlation Coefficient Estimation

The following between character genetic correlation coefficients were estimated using family-within-stand variance and covariance components:

- 1. greenhouse height (GHT) with height 1983 (HT2),
- 2. GHT with diameter 1983 (DIA),
- 3. height 1982 (HT1) with (HT2),
- date of leaf fall 1982 (LF1) with date of leaf fall 1983 (LF2),
- 5. HT2 with DIA,
- 6. HT2 with LF2,
- 7. HT2 with Melampsora leaf rust score 1983 (MLR),
- 8. HT2 with number of branches per decimeter 1983 (BRPD),
- 9. DIA with LF2,
- 10. DIA with MLR,
- 11. DIA with BRPD,
- 12. LF2 with MLR and
- 13. LF2 with BRPD.

The genetic correlation coefficient (r_G) between two characters (X and Y) is represented by the following formula:

$$r_{G_{XY}} = \frac{{}^{COV}_{F(S)}{}_{XY}}{[V_{F(S)_{X}} \cdot V_{F(S)_{Y}}]^{\frac{1}{2}}}$$
(Falconer, 1981), (4)

- where $COV_{F(S)}$ = family-within-stand covariance component of characters X and Y,
 - $V_{F(S)}_{X}$ = family-within-stand variance component of character X and
 - $V_{F(S)}$ = family-within-stand variance component of character Y.

Pooled locations data was utilized to estimate the necessary variance and covariance components. Standard errors of the genetic correlation coefficient estimates were computed. Figure 26, Appendix D contains the formula used in computing the standard errors of the genetic correlation estimates.

CHAPTER IV

RESULTS AND DISCUSSION

Means and Frequency Histograms

Nursery means for each character across locations and at each location, and greenhouse height means are presented in Tables XXIX and XXX, Appendix B. The highest five and lowest five ranking stand means for each character across locations and at each location, and for greenhouse height are presented in Tables XXXI to XXXVII, Appendix B. The highest seven and lowest seven ranking family-within-stand means for each character across locations and at each location, and for greenhouse height are presented in Tables XXXVIII to XLIV, Appendix B.

Combined locations family-plot mean frequency histograms for each nursery character and greenhouse height are presented in Figures 17 to 25, Appendix C. Height (HT2), diameter 1983 (DIA), date of leaf fall 1983 (LF2), number of branches per decimeter 1983 (BRPD) and greenhouse height (GHT) appear to be normally distributed. Height 1982 (HT1) and Melampsora leaf rust score 1983 (MLR) seem to be slightly skewed to the right, while date of leaf fall 1983 (LF1) seems to be slightly skewed to the left. Survival 1983 (SURV) plot means appear to be severely skewed to the left. For all characters a normal dis-

tribution of family-plot means was assumed and analyses of variance, F-tests, simple correlation coefficients (stand means with stand origin data) and heritabilities were computed.

Greenhouse Height

Mean greenhouse height (GHT) over the 10 replicates was 9.62 cm. These data were collected on August 24, 1982, making the seedlings 47 to 49 days old. Central and west Kansas, central and north Oklahoma and northwest Texas originating seedlings were the tallest at this stage (Figure 7 and Tables XXXI and XXXVIII, Appendix B). The shortest GHT seedlings were from central, south and east Texas and southwest Arkansas. The long day length (17 hours) of the greenhouse phase seems to have given seedlings of northern origin a distinct advantage in height growth through seven weeks.

Table IV presents the results of the analysis of variance procedure and F-tests for greenhouse height. Significant differences among stand and among family-within-stand means did exist, suggesting the presence of significant variability in GHT among stands and among families.

Height 1982

The mean height 1982 (HT1) over both locations was 25.3 cm. At the Norman nursery mean height 1982 was 27.4 cm and at Broken Bow it was 23.0 cm. The superiority of height 1982 at Norman was mostly



Figure 7. Greenhouse Height (cm) Pooled Stand Means

TABLE IV

GREENHOUSE HEIGHT ANALYSIS OF VARIANCE AND F-TEST RESULTS

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	9			
Stand	39	48.26	4.65*	39,119
Family (Stand)	119	10.37	1.94*	119,1410
Error	1410	5.34		

due to the achievement and maintenance of complete weed control, as opposed to partial control at Broken Bow.

Overall, the tallest stands and families after the first (1982) season were from south and east Texas, while the shortest originated in the Oklahoma panhandle, east Colorado and west Kansas (Figure 8 and Tables XXXI and XXXVIII, Appendix B). This situation was also apparent at each nursery location (Tables XXXIII, XXXV, XL and XLII, Appendix B), with the most southern stands and families ranked somewhat higher at Broken Bow than at Norman.

The analyses of variance and F-test results for height 1982 at Norman and at Broken Bow are presented in Table V. At each location differences among stand means were significant while differences among family-within-stand means were not significant. The analysis of variance and F-test results for height 1982 over both locations are presented in Table VI. As with the separate location analyses, the differences among stand means were significant; however, differences among family means were also significant. Apparently a significant amount of variation in first year height growth did exist among families, but it was not observed in the single location analyses. This is probably due to the increased sensitivity of the pooled analysis of variance, resulting from greater error degrees of freedom.

The location by stand interaction effect was significant for height 1982, while a location by family interaction did not exist (i.e. the location X family mean square was actually less than the error mean square). The significant location by stand interaction indicates that



Figure 8. Height 1982 (cm) Pooled Stand Means

TABLE V

		-ILSI RESULTS		
Norman Nursery	Degroop of	Mara G		
Variation	Freedom	Mean Square	f-Value	FDegrees of Freedom
Replicate	4			
Stand	39	411.99	5.66*	39,119
Family (Stand)	119	72.85	1.03	119,604
Error	604	70.43		,

HEIGHT 1982 ANALYSES OF VARIANCE AND F-TEST RESULTS

Note: * significant at the .05 probability level

Broken Bow Nurse	ry			
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4		********	
Stand	39	302.85	6.19*	39,119
Family (Stand)	119	48.94	1.14	119,609
Error	609	42.84		

TABLE VI

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8			
Stand	39	637.61	4.46*	44,116
Loc X Stand	39	77.28	1.68*	39,119
Family (Stand)	119	75.87	1.65*	119,119
Loc X Family (Stand)	119	45.93	0.81	119,1213
Error	1213	56.58		

HEIGHT 1982 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

either the stand ranking for HT1 was changing significantly between locations or the stand variance at one location was significantly different than at the other location (Lowe et al., 1982). The Fvalue for testing the hypothesis of equal stand variances between locations (i.e. $F = Norman MS_{Stand}$ / Broken Bow $MS_{Stand} = 1.36$) was not significant (.05); therefore, a change-in-rank type interaction seems more probable. However, in looking at the stand means it appears that a divergent-type interaction was occuring without significant changes in rank or significant differences in stand variances across locations. The stand means at Norman were greater than those at Broken Bow and the differences appear to increase as the means increase (Figure 9).

Height 1983

The mean height 1983 (HT2) over both nursery locations was 205.8 cm. At Norman, height 1983 was 223.5 cm and at Broken Bow it was 185.4 cm. Nursery site differences (e.g. fertility, soil structure, etc.) may outweigh weed control differences in explaining the superiority in mean HT2 at Norman. However, since HT2 is partially determined by HT1, any factor affecting HT1 also affects HT2. Therefore, weed control was probably an important factor through year two in Norman's superior height growth performance. In any case, the Norman nursery appears to be a better eastern cottonwood site than the Broken Bow nursery, except possibly in seasons of limited precipitation.



Figure 9. Divergent-Type Location X Stand Interaction, as Observed for Height 1982 (HT1)

Over both locations the tallest stands and families following two growing seasons originated from southeast Texas, west Arkansas and southeast Oklahoma (Figure 10 and Tables XXXI and XXXVIII, Appendix B). Stands 34 and 39 maintained their superior (#2 and #3) height 1982 ranking through 1983, while the southeast Oklahoma stands (i.e. 19, 20 and 21) improved immensely from 1982 to 1983. The poorest performing HT2 stands and families over both locations were from the Texas and Oklahoma panhandles, east Colorado and west Kansas. Most of these stands (and families) also ranked low for HT1 (Figure 8), which represents a reversal in rank compared to GHT (Figure 7). Apparently the long day effect of the greenhouse phase was beginning to deteriorate as stands and families of northern origin slowed in height growth under nursery conditions.

The situation observed at each nursery location was similar to the overall situation observed for height 1983. Southeast and southcentral Oklahoma stands and familes dominated the top ranks at Norman and south and east Texas stands and families ranked highest at Broken Bow (Tables XXXIII, XL, XXXV and XLII, Appendix B). It appears that a northward seed movement limit may have been reached. Mohn and Pauley (1969) reported that eastern cottonwood sources from 3° to 7° south of a Minnesota planting site performed better in height growth than did sources of local or further south (8° to 12°) origin. Norman, Oklahoma may be too harsh a climate (summer and winter) for seedlings of east and south Texas origin; however, Norman may be ideal (i.e.



Figure 10. Height 1983 (cm) Pooled Stand Means

for height growth) for seedlings from south and southeast Oklahoma. The low ranking HT2 stands and families were very similar for each location, being seedlings from the panhandles, east Colorado and west Kansas. It is clear that moving seed south or east is not advantageous to good eastern cottonwood growth.

The analyses of variance and F-test results for height 1983 at Norman and Broken Bow are presented in Table VII. At each nursery the differences among stand means were significant, while differences among family-within-stand means were significant at Broken Bow and not significant at Norman. The comparatively large error at Norman obscured the family differences at the .05 probability level, but at the .10 level, significant differences among family means did exist. This large error could be due to many factors, including less site and irrigation uniformity at Norman.

The analysis of variance for height 1983 and F-test results over both locations are presented in Table VIII. Variances due to stand and location by stand interaction effects were significant, while family and location by family interaction effects were not significant. Apparently the large error mean square at Norman caused the pooled location analysis to fail in detecting significant differences among family means.

The F-statistic for testing equal stand variances between locations was significant at the .05 probability level. Therefore, some of the significance of the location by stand interaction may be due to the difference in stand variances between locations. A ranking of the

TABLE VII

HEIGHT 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery							
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom			
Replicate	4						
Stand	39	11255.12	3.87*	39,119			
Family (Stand)	119	2910.38	1.18	119,597			
Error	597	2462.98					

Note: * significant at the .05 probability level

Broken Bow Nurser	<u>y</u>			
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4			
Stand	39	19464.41	9.76*	39,119
Family (Stand)	119	1993.81	1.44*	119,590
Error	590	1383.30		

TABLE VIII

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8			
Stand	39	26707.35	4.29*	45,95
Loc X Stand	39	4014.01	1.84*	39,119
Family (Stand)	119	2718.58	1.24	119,119
Loc X Family (Stand)	119	2186.17	1.13	119,1187
Error	1187	1926.18		

HEIGHT 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

HT2 stand means, at each location, reveals that changes in rank appear from one location to the other (Tables XXXIII and XXXV, Appendix B). Most apparent is the upward movement in rank of the south and east Oklahoma (stands 19, 20 and 21) and west Arkansas (stand 12) stands from Broken Bow to Norman. It is probable that both differences in stand variances and stand rankings combined to produce the significant location by stand interaction effect. Significant genotype by environment interactions are common in eastern cottonwood, especially when tested at environmentally diverse sites (Randall and Mohn, 1969; Mohn and Randall, 1973). Change-in-rank interactions suggest that the breeding population be divided into sub-populations each being selected and bred for specific sites; or the breeding population be selected and bred for a wide range of sites (Mohn and Randall, 1973). Ying and Bagley (1976a) argue that breeding specialized populations for specific areas is the optimal procedure for eastern cottonwood improvement.

Diameter 1983

The mean diameter 1983 (DIA) over both locations was 14.9 mm. Mean diameter 1983 was 16.1 mm at Norman and 13.5 mm at Broken Bow. Site and weed control differences between locations were, again, probably the major causes of Norman's superiority in mean second year diameter. Over both locations, stands and families originating in southeast Texas, southwest Arkansas and southeast Oklahoma ranked the highest for DIA (Figure 11 and Tables XXXI and XXXVIII, Appendix B).



Figure 11. Diameter 1983 (mm) Pooled Stand Means

The lowest ranking DIA stands and families came from the Texas and Oklahoma panhandles, east Colorado and west Kansas. This is a similar trend to that of height 1983 (Figure 10). At Norman the best second year diameter stands and families were from southeast and east Oklahoma, southwest Arkansas and southeast Texas, while at Broken Bow seedlings of southeast Texas origin were alone at the top (Tables XXXIII, XL, XXXV and XLII, Appendix B). These results indicated that moving eastern cottonwood seed north and/or west is advantageous for increasing diameter growth; however, a limit to this movement definitely exists.

The smallest DIA progenies, at each location, originated from parents of the Texas and Oklahoma panhandles, west Texas and east Colorado. This trend was also suggested for HT1, HT2 and DIA over locations. While it is apparent that north and/or westward movement (to a limit) of cottonwood seed seems advantageous, it appears definite that south and/or eastward movement is detrimental for rapid growth. The slowest height and diameter growing seedlings at each location originated in the northwest area of the sampled region (stands 1,2,3, 7,13 and 17).

The individual location analyses of variance and F-tests for diameter 1983 are presented in Table IX. Differences among stand and among family-within-stand means were significant at Norman and Broken Bow, suggesting real differences in diameter growth rate from stand-tostand and family (within stand)-to-family (within stand) of this cottonwood population.

TABLE IX

DIAMETER 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery							
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom			
Replicate	4						
Stand	39	93.22	4.53*	39,119			
Family (Stand)	119	20.56	1.30*	119,597			
Error	597	15.86					

Note: * significant at the .05 probability level

Broken Bow Nursery				
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4			
Stand	39	190.96	11.41*	39,119
Family (Stand)	119	16.74	1.55*	119,590
Error	590	10.77		

The analysis of variance and F-test results over both locations for diameter 1983 are presented in Table X. The effects of stand, family and location by stand interaction were significant, while the location by family interaction effect was not significant. The F-value for testing equal stand variances between locations was significant at the .05 probability level. As with height 1983, this seems to indicate that a portion of the stand by location interaction was due to differences in stand-caused variance between locations. The stand variance at Broken Bow was significantly larger than the stand variance at Norman. However, stand means ranked by location show changes between locations, specifically in the upper half of the rankings at each nursery (Tables XXXIII and XXXV, Appendix B). This is similar to the situation for height 1983. Seedlings of south and southeast Oklahoma origin ranked the highest at Norman, while at Broken Bow seedlings of southeast Texas origin were on top. The lower half of the rankings were similar across locations, with stands 1, 2, 7 and 17 at the bottom.

Date of Leaf Fall 1982

The mean date of leaf fall 1982 (LF1) over both locations was 31 days (after November 1, 1982). At Norman mean date of leaf fall 1982 was 38 days and at Broken Bow it was 24 days. The seedlings at Broken Bow were apparently forced into early dormancy and subsequent early leaf fall by the more severe weed competition. Jokela and Mohn

TABLE X

DAIMETER 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8			
Stand	39	248.73	4.59*	43,90
Loc X Stand	39	35.49	2.32*	39,119
Family (Stand)	119	22.00	1.44*	119,119
Loc X Family (Stand)	119	15.31	1.15	119,1187
Error	1187	13.33		

(1976) reported that growth cessation and date of leaf fall in eastern cottonwood may be hastened by drought and other adverse growing conditions. This may also help to explain the slower height and diameter growth, through two years, at Broken Bow. Not only did the light, nutrient and water competition cause an apparent decrease in the growth rate, it also caused a decrease in the effective length of Broken Bow's growing season. When considering climatological data, Broken Bow should have a longer growing season (Table XXVII, Appendix A); however, the stress placed on the Broken Bow seedlings by the more severe weed population resulted in Broken Bow having a shorter growing season than Norman.

Over both locations, stands and families with the latest date of leaf fall 1982 were from southeast Texas (Figure 12 and Tables XXXII and XXXIX, Appendix B). Of the farthest south and east stands studied, only stand 38 did not rank with the latest date of leaf fall group. The earliest date of leaf fall 1982 stands and families originated from the Oklahoma panhandle, east Colorado and west and central Kansas. At the individual nurseries both the late and early leaf fall stands and families were very similar to the combined nursery situation (Tables XXXIV,

The environmental differences of the two nursery sites does not appear to effect the relative LFI rank of stands or families; however, the magnitude of the stand and family mean differences were greatly reduced at Broken Bow as compared to Norman.



Figure 12. Date of Leaf Fall 1982 (days past 11-1-82) Pooled Stand Means
The analyses of variance and F-test results for date of leaf fall 1982 at Norman and at Broken Bow are presented in Table XI. Significant differences among stand and among family means appeared at each location, suggesting that a large amount of stand and family variation in first year date of leaf fall is present in the sampled eastern cottonwood population.

The analysis of variance and F-test results for date of leaf fall 1982 over both locations is presented in Table XII. As found in the individual location analyses, differences among stand and among family means were significant. The two interaction effects were also significant, suggesting a change-in-stand and in-family rank between locations. However, the F-value for testing equal stand variances between locations was significant (.05). Therefore, much of the location by stand interaction effect appears to be due to unequal stand variances (between locations) and not to stand rank changes between locations.

On the contrary, the F-statistic for testing unequal familywithin-stand variances between locations was not significant (i.e. $F = Norman MS_{Family(Stand)} / Broken Bow MS_{Family(Stand)} = 1.05$), suggesting that a significant change-in-family (within stand) rank may have occurred between locations. Different families within the same high and low ranking stands occupy the high and low ranking positions at the different nurseries. Therefore, the LF1 stand means were not changing positions between locations, while the LF1 familywithin-stand means were changing positions.

TABLE XI

DATE OF LEAF FALL 1982 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery							
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom			
Replicate	4	3					
Stand	39	414.90	4.42*	39,119			
Family (Stand)	119	93.91	2.32*	119,605			
Error	605	40.42					

Note: * significant at the .05 probability level

Broken Bow Nursery	-			
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4			
Stand	39	1634.74	18.34*	39,119
Family (Stand)	119	89.13	1.64*	119,612
Error	612	54.42		

TABLE XII

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1	,		
Replicate (Loc)	8			
Stand	39	1649.94	3.36*	42,62
Loc X Stand	39	397.39	5.73*	39,119
Family (Stand)	119	113.77	1.64*	119,119
Loc X Family (Stand)	119	69.36	1.46*	119,1217
Error	1217	47.47		

DATE OF LEAF FALL 1982 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

Date of Leaf Fall 1983

The mean date of leaf fall 1983 (LF2) over both locations was 25 days (after October 31, 1983). The mean LF2 at Norman was 30 days and it was 20 days at Broken Bow. These means were 6, 8 and 4 days earlier than the date of leaf fall means for the first year over locations, at Norman and Broken Bow, respectively. The shipment and outplanting of seven week old greenhouse grown seedlings in late August and early September may have disrupted the seedlings' physiological processes of growth cessation and dormancy, causing an abnormal delay (during the first season) of the onset of dormancy. Another possible explanation of the difference in mean dates of leaf fall between years is that the lack of irrigation and a dry late summer during 1983 may have caused the onset of dormancy to be earlier in 1983 than in 1982.

Over both locations southeast Texas stands and families were the latest to reach second year date of leaf fall, while Texas and Oklahoma panhandle, east Colorado and west Kansas stands and families were the earliest (Figure 13 and Tables XXXII and XXXIX, Appendix B). A similar situation was observed at each location (Tables XXXIV, XLI, XXXVI and XLIII, Appendix B). This north-to-south (early date to late) trend agrees with first year date of leaf fall (LF1) data of this study and previous results of other cottonwood research (Jokela and Mohn, 1976). Pauley and Perry (1954) determined that the onset of dormancy is dependent on photoperiod. With day length decreasing in the fall, a certain length of night time darkness triggers the



Figure 13. Date of Leaf Fall 1983 (days past 10-31-83) Pooled Stand Means

initiation of the dormancy process in the tree. Southern genotypes respond to longer dark periods; therefore, when moved north they enter dormancy later because of the northern latitude's longer days (shorter nights).

The analyses of variance and F-test results for date of leaf fall 1983 at each location and over locations are presented in Tables XIII and XIV. Significant differences were found at each location among stand and among family-within-stand means. As with LF1, LF2 data also contained a significant amount of stand and family variation. The combined location analysis revealed significant differences among stand, among family and among location by stand interaction means; however, the location by family interaction effect was not significant. The F-statistic for testing equal stand variances between locations was significant at the .05 probability level, which suggests that the high significance of the location by stand interaction effect was due in part to the difference in stand variances between locations. Visually, no significant stand rank changes for LF2 appeared to occur from one location to the other.

Melampsora Leaf Rust Score 1983

The mean Melampsora leaf rust score 1983 (MLR) over both locations was 30 percent. Only a two percent difference in mean Melampsora rust score occurred between the two locations--29 percent at Norman and 31 percent at Broken Bow. The most severely infected seedlings, over both locations, originated in the northwest area of the studied

TABLE XIII

DATE OF LEAF FALL 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery						
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom		
Replicate	4					
Stand	39	794.24	8.61*	39,119		
Family (Stand)	119	92.24	1.68*	119,597		
Error	597	54.76				

Note: * significant at the .05 probability level

Broken Bow Nursery						
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom		
Replicate	4					
Stand	39	1631.38	21.46*	39,119		
Family (Stand)	119	76.02	2.85*	119,590		
Error	590	26.69				

Note: * significant at the .05 probability level

TABLE XIV

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8	л х		
Stand	39	2154.52	5.62*	40,76
Loc X Stand	39	270.51	5.74*	39,119
Family (Stand)	119	121.08	2.57*	119,119
Loc X Family (Stand)	119	47.12	1.15	119,1187
Error	1187	40.81		

DATE OF LEAF FALL 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

region, including stands 1, 2, 3, 7 and 8 (Figure 14 and Tables XXXII and XXXIX, Appendix B). Seedlings having the most apparent Melampsora rust resistance, overall and at each location, were from southeast Texas (stands 34, 36, 39 and 40) and southwest Arkansas (stand 22). Three possible explanations are apparent to explain the high MLR of northwestern stands and families and the low MLR of southeastern stands and families.

First, the arid climate of the northwest area of the sampled cottonwood population is not conducive to rust survival and proliferation. Therefore, the cottonwood of the northwestern stands have not been subjected to severe Melampsora leaf rust infection, resulting in little or no natural selection for Melampsora rust resistance. Contrarily, the southeast area of the study region is moist, providing a good environment for rust proliferation. Hence, the cottonwood of the southeastern stands have been naturally selected for Melampsora rust resistance for several generations. This obviously results in the southeastern stands and families being more resistant to Melampsora leaf rust than the northwestern stands and families.

Second, the incidence of Melampsora leaf rust may be purely influenced by environmentally induced physiological phenomena, such as the onset of dormancy (Jokela and Mohn, 1976; Cooper and Filer, 1976). Stands and families from the northwest tended to have early dates of leaf fall (LF1 and LF2) as well as high Melampsora rust scores (MLR). This early leaf fall, resulting from an associated early senescence, may result in decreased resistance to Melampsora rust infection.



Figure 14. Melampsora Leaf Rust Score (%) 1983 Pooled Stand Means

Third, increased Melampsora leaf rust resistance of the southeastern stands and families may be the result of gene flow and accumulation (Cooper and Filer, 1976). Eastern cottonwood's natural linear distribution along watersheds results in downstream gene flow. The river systems of the studied region flow northwest to southeast; therefore, rust resistance determining alleles will tend to accumulate southeast of their origin. Stands in the southeast have the "luxury" of incorporating new (valuable) alleles, while northwestern stands do not. This indicates that moving seed and vegetative cuttings against the direction of gene flow will result in plantings with more Melampsora leaf rust resistance than local or northwest-of-local reforestation material. Results of this study have shown this to also be true for increasing first and second year height (HT1 and HT2) and second year diameter (DIA) and for delaying first and second year dates of leaf fall (LF1 and LF2).

The Norman and Broken Bow analyses of variance and F-test results for Melampsora leaf rust score 1983 are presented in Table XV. Significant differences among stand means at each location were found, suggesting the presence of a large amount of geographic (among stand) Melampsora rust resistance variability within this portion of eastern cottonwood's range. Differences among family-within-stand means were significant at Broken Bow, but not significant at Norman. The large error mean square at Norman lessened the opportunity of detecting any real differences among family means. Added environmental variation caused by collecting MLR data over two days at Norman (compared

TABLE XV

MELAMPSORA LEAF RUST SCORE 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery				
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4			
Stand	39	4517.61	12.29*	39,119
Family (Stand)	119	367.55	1.02	119,596
Error	596	361.45		

Note: * significant at the .05 probability level

Broken Bow Nursery						
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom		
Replicate	4					
Stand	39	6929.09	19.47*	39,119		
Family (Stand)	119	355.85	2.22*	119,586		
Error	586	160.22				

to one day at Broken Bow) is a probable cause of the larger error at Norman.

The analysis of variance and F-test results over both locations is presented in Table XVI. Melampsora leaf rust score 1983 and survival 1983 were the only characters that did not show significant location effects at the .05 probability level ($F_{MLR} = 0.63$ with 1 and 9 degrees of freedom and $F_{SURV} = 4.36$ with 1 and 12 degrees of freedom). However, the location effect for survival 1983 was significant at the .10 probability level.

Stand, family and location by stand interaction effects were all significant. The significance of family variation, in the combined analysis, supports the idea that family variation was probably significant at Norman but the large error erased the possibility of detection. The F-value for testing equal stand variances between locations was not significant (.05), which suggests that a change-inrank location by stand interaction has occurred. However, in looking at individual location MLR stand means, no obvious interaction can be observed or explained. The location by family interaction effect was not significant.

Number of Branches per Decimeter 1983

The mean number of branches per decimeter 1983 (BRPD) was 0.87 over locations, 1.07 at Norman and 0.64 at Broken Bow. The large differences in nursery means is probably due to the nursery differences in weed control success and site productivity. The Norman planting,

TABLE XVI

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8			
Stand	39	10672.29	8.96*	41,87
Loc X Stand	39	774.40	2.81*	39,119
Family (Stand)	119	447.75	1.62*	119,119
Loc X Family (Stand)	119	275.64	1.05	119,1182
Error	1182	261.69		

MELAMPSORA LEAF RUST SCORE 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

with complete weed control and being a better cottonwood site, produced more branches per length of main stem than did Broken Bow. Space and sunlight competition appeared to inhibit the Broken Bow seedlings' ability to produce branches.

Stands from west Texas (i.e. 18 and 23) and west Oklahoma (i.e. 14 and 19) produced seedlings with the most branches per decimeter of main stem at Norman, while stands from southwest Texas (i.e. 33, 38 and 41) and stands 18 and 19 produced seedlings with the highest BRPD at Broken Bow (Tables XXXIV and XXXVI, Appendix B). Over locations, stands 18 and 19 maintained their number one and two rankings and a general west-to-east (more BRPD to less) trend prevailed (Figure 15 and Table XXXII, Appendix B).

The analyses of variance and F-test results for number of branches per decimeter 1983 at each location and over locations are presented in Tables XVII and XVIII. Significant stand and family-within-stand variation was found in both the individual and pooled location analyses. The location by stand interaction was also significant, while the location by family interaction was not significant. The increase in rank of southwest Texas stands (i.e. 33, 38 and 41), from Norman to Broken Bow, apparently altered the stand rankings enough to detect a significant location by stand interaction effect (Tables XXXIV and XXXVI, Appendix B). The stand variances between locations were not significantly different, supporting the hypothesis of a significant rank changing interaction.



Figure 15. Number of Branches per Decimeter 1983 Pooled Stand Means

TABLE XVII

NUMBER OF BRANCHES PER DECIMETER 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery				
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Replicate	4			
Stand	39	0.6615	3.92*	39,119
Family (Stand)	119	0.1687	2.17*	119,597
Error	597	0.0778		

Note: * significant at the .05 probability level

Broken Bow Nursery					
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom	
Replicate	4				
Stand	39	0.5895	3.26*	39,119	
Family (Stand)	119	0.1809	2.19*	119,590	
Error	590	0.0826			

TABLE XVIII

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1	,		
Replicate (Loc)	8			
Stand	39	0.9579	1.86*	45,112
Loc X Stand	39	0.2930	3.56*	39,119
Family (Stand)	119	0.2676	3.25*	119,119
Loc X Family (Stand)	119	0.0824	1.03	119,1187
Error	1187	0.0802		

NUMBER OF BRANCHES PER DECIMETER 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

Survival 1983

Percent survival (SURV) through the 1983 growing season over both nursery locations was 73.3. Survival was 79.4 percent at the Norman nursery and 67.5 percent at Broken Bow. Some of the mortality at both locations occurred during the period immediately following outplanting. Irrigation problems resulted in too much water in some sections and too little water in others. The superior survival percentage at Norman can probably be explained by the maintenance of complete weed control, as opposed to partial control at Broken Bow. Eastern cottonwood is very shade intolerant, requiring full sunlight to survive and grow (Fowells, 1965).

Percent survival by stands over both locations ranged from 87.5 for stand 39 to 57.6 for stand 1. Ranges in percent survival at the individual nurseries were from 91.7 (stand 18) to 63.2 (stand 19) at Norman, and from 88.3 (stand 41) to 36.3 (stands 1 and 7) at Broken Bow. Table XXXVII, Appendix B presents the highest and lowest five ranking stands for survival 1983 at each location and over both locations. The highest and lowest seven ranking families for percent survival 1983 at each location and across locations are given in Table XLIV, Appendix B.

Overall, the best surviving stands and families originated in south Texas and west Arkansas (Figure 16). The poorest stands and families came from northwest Texas, northwest Oklahoma, west and



Figure 16. Survival 1983 (%) Pooled Stand Means

central Kansas and east Colorado. However, when looking at the Norman nursery results, northwest Texas, northwest Oklahoma and Kansas stands and families survived quite well and south and southeast Oklahoma and some Texas stands and families did poorly. This may be expected since the Norman nursery environment is more similar to the panhandle environment than to southeast Texas. At Broken Bow, survival percent by stands and families looks quite similar to the pooled location means, with the south and east Texas stands and families surviving best.

The analyses of variance and F-test results for survival 1983 (SURV) at each nursery and over nurseries are presented in Table XIX and XX. Differences among stand means were significant at Broken Bow, but not at Norman or overall. Differences among family-withinstand means were not significant at either location or over locations. The location by stand interaction effect was significant, while the location by family-within-stand effect was not. The F-value for testing equal stand variances between locations was significant (.05), suggesting that a portion of the location by stand interaction effect was due to the difference in stand variances between nurseries.

The significant stand effect at Broken Bow may relate to that site's adverse growing conditions (i.e. weed competition and poorer cottonwood site). Natural selection for survival within the nursery environments may have been stronger at Broken Bow than at Norman;

TABLE XIX

SURVIVAL 1983 ANALYSES OF VARIANCE AND F-TEST RESULTS

Norman Nursery								
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom				
Replicate	4							
Stand	39	873.96	1.43@	39,119				
Family (Stand)	119	609.97	0.85	119,624				
Error	624	714.91						

Note: @ significant at the .10 probability level

Broken Bow Nursery							
Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom			
Replicate	4						
Stand	39	3178.79	4.04*	39,119			
Family (Stand)	119	786.34	1.21@	119,629			
Error	629	652.13					

Note: * significant at the .05 probability level @ significant at the .10 probability level

TABLE XX

Source of Variation	Degrees of Freedom	Mean Square	F-Value	FDegrees of Freedom
Location	1			
Replicate (Loc)	8			
Stand	39	1513.85	0.69	78,61
Loc X Stand	39	2538.90	3.55*	39,119
Family (Stand)	119	680.64	0.95	119,119
Loc X Family (Stand)	119	715.67	1.05	119,1253
Error	1253	683.39		

-

SURVIVAL 1983 POOLED ANALYSIS OF VARIANCE AND F-TEST RESULTS

hence, the significant differences among Broken Bow stand means. However, irrigation through seedling establishment no doubt reduced the selection pressures for survival at both sites; thus, minimizing the differences.

Simple Correlation Coefficients of Stand Means with Stand Origin Data

Pearson correlation coefficients of the pooled stand means for each character with several stand origin environmental and geographical variables are presented in Table XXI. These simple correlation coefficients represent a quantification of the presence or absence of geographic and/or environmental (among stand) variation patterns.

Stand means for number of branches per decimeter 1983 were correlated with longitude (r = .44) and mean annual precipitation (r = -.44). Stands from further west and from areas of less annual precipitation produced seedlings with more branches per length of main stem than did other stands. Stand longitudes and mean annual precipitation values were also strongly correlated (r = -.90), suggesting that environments with limiting moisture tend to be further west and they produce shorter, branchier eastern cottonwood seedlings as a result of conservative growth in a dry environment (Figures 10 and 15). Posey (1969) also found a west-to-east (more branches per foot to less) trend in his study of one year old cottonwoods from Oklahoma originating vegetative cuttings.

TABLE XXI

PEARSON CORRELATION COEFFICIENTS OF STAND MEANS WITH STAND ORIGIN DATA

CHARACTER	Latitude	Longitude	Mean ∦ Frost Free Days	Mean Annual Precip.	Elevation	Mean Annual Min. Temp.	Mean Annual Max. Temp.
GHT	.45*	.38*	41*	43*	.38*	48*	02
HT1	88*	58*	.85*	.60*	74*	.61*	.47*
HT2	57*	78*	.67*	.69*	85*	.45*	.61*
DIA	70*	82*	.78*	.77*	90*	.53*	.60*
LF1	91*	59*	.89*	.61*	77*	.69*	.47*
LF2	89*	59*	.89*	.63*	77*	•64*	.43*
MLR	.75*	.83*	82*	79*	.91*	58*	51*
BRPD	.03	.44*	17	44*	.24	03	.22
SURV	48*	63*	.55*	.58*	67*	.28	.39*

Note: * significantly different from zero at the .05 probability level

Greenhouse height stand means were significantly correlated with latitude (r = .45), longitude (r = .38), mean annual precipitation (r = -.43), elevation (r = .38), mean annual minimum temperature (r = -.48) and mean number of frost free days (r = -.41). The trend suggested from these coefficients indicates that seven week old cottonwood seedlings will tend to be taller if they originate from stands further north and west (Figure 7). In addition, these stands will tend to be in areas of lower mean annual precipitation, higher elevation, lower mean annual minimum temperature and shorter season between spring and fall frosts. The long day length (17 hours) of the greenhouse phase may have favored the seedlings of northern origin. However, seedlings originating in colder and drier climates may benefit from some advantage in rapid, early growth as opposed to seedlings from warmer and more moist climates.

Height 1982 and 1983 (HT1 and HT2) stand means were strongly and positively correlated with mean annual precipitation, mean annual minimum and maximum temperatures and mean number of frost free days. First and second year heights were negatively correlated with latitude, longitude and elevation. A definite west-to-east and north-to-south (short height to tall) geographic pattern of variation was evident. The north-to-south trend appears to be more important for HT1, while the west-to-east trend seems more important for HT2. However, for both characters a northwest-to-southeast trend seems to best explain the pattern of variation (Figures 8 and 10).

Stand means for diameter 1983 were strongly correlated to all geographical and environmental variables. The same northwest-tosoutheast trend of HT1 and HT2 was apparent for second year diameter, with the west-to-east (small diameter to large) being more important (Figure 11). This was described by the large, negative correlation coefficients of DIA with elevation (r = -.90) and longitude (r = -.82).

Survival 1983 stand means were strongly and negatively correlated with latitude and longitude, suggesting west-to-east and north-tosouth trends (low percent survival to high), even though the analysis of variance failed to detect significant differences among survival stand means (Table XX). As for DIA and HT2, the west-to-east pattern of survival 1983 seems more clearly defined than the north-to-south. A positive correlation with mean annual precipitation and a negative correlation with elevation also give the west-to-east trend support, as elevation was positively correlated with longitude (r = .90). However, as was the case for HT1, HT2 and DIA a northwest-to-southeast trend appears to best describe the survival variation pattern (Figure 16).

Stand means for first and second year date of leaf fall (LF1 and LF2) followed the same pattern of variation as did survival 1983, DIA, HT2 and HT1. However, the north-to-south (early date to late) trend appears to be more important than the west-to-east for both years' date of leaf fall (Figures 12 and 13). LF1 and LF2 were most

strongly correlated with latitude (r = -.91 and -.89, respectively) and mean number of frost free days (r = .89 for both). Dates of early fall frost are obviously important agents of selection for date of leaf fall, as stands from areas with shorter growing seasons (late spring and early fall frosts) tended to produce seedlings with earlier dates of leaf fall.

Melampsora leaf rust score 1983 stand means exhibited a similar trend of variation as did the growth and leaf fall characters and second year survival. A strong northwest-to-southeast trend (high percent infection to low) was apparent (Figure 14). Seedlings originating from the north and west were much more susceptible to Melampsora leaf rust than were seedlings from the south and east. These results are similar to reports by Theilges and Adams (1975), Cooper and Filer (1976), Jokela and Mohn (1976) and Friend (1981), who all found a north-to-south (more susceptible to less) Melampsora leaf rust resistance trend.

The significant differences among stand means for GHT, HT1, HT2, DIA, LF1, LF2, MLR and BRPD (Tables IV, VI, VIII, X, XII, XIV, XVI and XVIII) do not appear to be random, but follow a describable pattern of clinal (continuous) variation. Within the southwestern portion of eastern cottonwood's native range a northwest-to-southeast (smaller to larger) geographic trend was evident for first and second year height (HT1 and HT2), second year diameter (DIA) and first and second year dates of leaf fall (LF1 and LF2) and second year survival (SURV).

A northwest-to-southeast (larger means to smaller) trend was evident for greenhouse height (GHT) and second year Melampsora leaf rust score (MLR). A west-to-east (more branches per decimeter to less) pattern of clinal variation was apparent for second year number of branches per decimeter of main stem (BRPD).

Heritability and Genetic Variance

Component Estimates

Family mean narrow sense heritability estimates (h^2) and standard errors (se) of the estimates are presented in Table XXII. First and second year dates of leaf fall (LF1 and LF2), Melampsora leaf rust score (MLR) and number of branches per decimeter (BRPD) were all highly heritable, with exception of MLR at Norman $(h^2 = .02)$. This estimate is extremely low when compared to the Broken Bow $(h^2 = .55)$ and pooled locations' estimates $(h^2 = .38)$. The large standard error $(\pm .14)$ associated with the Norman MLR heritability estimate indicates the probable lack in precision of this estimate. The characters LF1, LF2, MLR and BRPD are apparently under strong genetic control. Farmer (1966) reported that morphological and phenological characters of lower Mississippi Valley eastern cottonwood appeared to be under simple genetic control.

Improvement of LF1, LF2, MLR and/or BRPD could be efficiently achieved by simple mass selection. Since geographic (stand) variation is also very significant in these characters, selections should

TABLE XXII

FAMILY MEAN HERITABILITY ESTIMATES AND STANDARD ERRORS OF THE ESTIMATES

CHARACTER	Norman	Broken Bow	Pooled
	$h^2 \pm se$	h ² ± se	$h^2 \pm se$
GHT	X	X	.49 ± .07
HT1	.03 ± .14	.12 ± .12	.35 ± .10
HT2	.15 ± .12	.31 ± .10	.19 ± .15
DIA	.23 ± .11	.36 ± .09	.30 ± .13
LF1	.57 ± .06	.39 ± .09	.39 ± .11
LF2	.41 ± .08	.65 ± .05	.61 ± .07
MLR	.02 ± .14	.55 ± .06	.38 ± .11
BRPD	.54 ± .07	.54 ± .06	.69 ± .06
SURV	.00 ± .17	.17 ± .12	.00 ± .14

be limited to the most favorable stands. However, by basing selections on stand means the family mean heritability estimates will not be valid in genetic response predictions. The importance of the stand variance component for LF1, LF2, MLR and BRPD can be seen in Table XXIII. Stand variation is expecially important for LF1, LF2 and MLR.

First and second year height (HT1 and HT2) and second year diameter (DIA) heritability estimates were low to moderate. Farmer and Wilcox (1965) reported heritability estimates for first year height and diameter to be 0.93 and 0.56, respectively, and the estimates for third year height and diameter to be 0.35 and 0.16, respectively. In this study, DIA appears to be more highly heritable than either HT1 or HT2.

Improvement in seedling height and diameter growth rate requires a more sophisticated selection method than is necessary for improving date of leaf fall, Melampsora rust resistance and number of branches per length of main stem. Selection based on family and individual performance in replicated progeny tests from several locations would be necessary to make reasonable gains in juvenile height and diameter growth characters.

Second year percent survival was very lowly heritable. Familywithin-stand variance component estimates at Norman and over nurseries were negative, resulting in heritability estimates of zero. Selection for survival improvement under natural Oklahoma conditions would

TABLE XXIII

STAND AND FAMILY VARIANCE COMPONENTS AS A PERCENT OF THE TOTAL PHENOTYPIC VARIANCE

CHARACTER	Norman		Broken Bow		Pooled	
	Stand	Family	Stand	Family	Stand	Family
GHT	х	X	Х	Х	14.1	7.5
HT1	20.0	0.6	23.0	2.2	18.4	4.1
HT2	14.7	3.1	38.0	5.3	22.0	2.1
DIA	18.5	4.8	43.5	5.9	26.0	3.4
LF1	24.5	16.3	56.5	5.1	29.9	4.4
LF2	37.1	7.9	69.0	-8.7	43.7	7.1
MLR	37.6	0.2	63.5	7.6	45.5	3.2
BRPD	21.1	15.5	17.3	16.7	10.2	15.8
SURV	1.8	0.0	15.1	3.4	0.0	0.0

require family and individual information from several non-irrigated test locations. First year irrigation was essential in this study to ensure an adequate population of surviving trees for two year data and future research.

Greenhouse height was highly heritable $(h^2 = .49)$. However, Wright (1976) emphasizes that heritability estimates based on one location are overestimated, because the family variance component includes location by family interaction variance. This suggests that the pooled heritability estimates (excluding GHT) of this study are most realistic, when considering the southwestern range of eastern cottonwood and Oklahoma planting sites.

Stand and family-within-stand variance components as a percent of the total phenotypic variance (Equations 2 and 3) are presented in Table XXIII. For all characters studied, except BRPD, at each location and over locations the stand variance component was at least 50 percent larger than the family component. The family variance component was larger than the stand component for BRPD over locations and nearly as large at the individual nursery sites. This supports the F-test results in indicating that considerable variation in eastern cottonwood juvenile characters exists among stands of the southern Great Plains. The relatively non-continuous distribution of cottonwood in the study area (i.e. along rivers and streams) and therefore restricted gene flow has allowed the gene frequencies of individual stands to diverge from other stands, creating obvious geographic variation.

Genetic Correlation Coefficient Estimates Between Selected Characters

Estimates of the true genetic correlation coefficients (r_{G}) and standard errors (se) of these estimates are presented in Table XXIV. Thirteen of the possible 28 between character coefficients were estimated. These 13 correlations were judged to be most valuable for genetic interpretation and most practical for future use in an eastern cottonwood breeding program.

Greenhouse height (GHT) and height 1982 (HT1) were both negatively, genetically correlated with height 1983 (HT2), suggesting that taller seven week and one season old cottonwood seedlings will tend to result in shorter two year old seedlings. Three possibilities exist to explain these correlation coefficients:

 The greenhouse height advantage of the northern seedlings (possibly due to long day lengths) continued through the first season, causing HTl to be negatively correlated with HT2;

2. The greenhouse-to-nursery environmental change caused a reversal in the height growth trend (i.e. taller northwestern seedlings to taller southeastern seedlings) that took two seasons to complete; and

3. Northwestern seedlings have been naturally selected for rapid early growth (seven weeks) as a vital fitness character.

A small negative genetic correlation coefficient was also found for GHT with DIA ($r_G = -.13$). This coefficient, as the GHT and HT1

TABLE XXIV

GENETIC CORRELATION COEFFICIENT ESTIMATES BETWEEN SELECTED CHARACTERS AND STANDARD ERRORS OF THE ESTIMATES

	HT2	DIA	LF2	MLR	BRPD
	r _G ± se				
GHT	75 ± .36	13 ± .27	-		
HT1	16 ± .48				
HT2		.68 ± .20	.26 ± .30	.24 ± .41	.39 ± .24
DIA			.31 ± .23	$38 \pm .34$.69 ± .14
LF1			.68 ± .16		
LF2				55 ± .17	.37 ± .14

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with HT2 coefficients was probably confounded by the continuation of the greenhouse growth trend or the greenhouse-to-nursery environmental change; therefore, no practical relationship between seven week old seedling height and second year diameter was apparent.

Second year date of leaf fall was positively, genetically correlated with second year height ($r_{\rm G}$ = .26) and diameter ($r_{\rm G}$ = .31); however, these coefficients are not large and their standard errors are fairly large (± .30 and .23, respectively). A genetic relationship does possibly exist between increased height and diameter growth with later date of leaf fall, but it was not readily apparent from these results.

Melampsora leaf rust score was positively, genetically correlated with HT2 and negatively with DIA. Seedlings with tall height and small diameter are apparently more susceptible to Melampsora leaf rust infection than shorter and larger diameter seedlings. An alternative interpretation is that juvenile height growth is not adversely affected by severe rust infection, while diameter is adversely affected. The rust infection peaks late in the growing season, possibly after the end of stem elongation but before the termination of radial growth. Therefore, severely infected seedlings are denied the opportunity of a full season's increment.

Early date of leaf fall 1983 was genetically correlated with serious Melampsora leaf rust infection in 1983. Two explanations can be put forth; either individuals that enter dormancy early are
more susceptible to rust infection or individuals that are more susceptible to rust infection drop their leaves earlier. Jokela and Mohn (1976) report that eastern cottonwood seedlings which shut down and enter dormancy early are more susceptible to severe Melampsora leaf rust infection than are seedlings that continue growing late into the fall.

Number of branches per decimeter 1983 was strongly and positively, genetically correlated with diameter 1983; trees with larger diameters were likely to produce more branches per length of main stem than were trees with smaller diameters. BRPD was also positively, genetically correlated with second year height (HT2) and date of leaf fall (LF2), although not as strongly as with DIA. This seems to contradict the BRPD pattern of variation, which indicated that shorter, smaller diameter trees produce more branches per length of main stem and originate in western stands. However, genetic correlation coefficients measure the correlation between the additive genetic values (breeding values) of the two characters--BRPD with DIA and BRPD with HT2 (Falconer, 1981). Phenotypic (simple) correlation coefficients (which suggested that shorter and smaller diameter trees will produce more branches per decimeter of main stem) are not useful in determining the genetic correlation between characters, because environmental and non-additive genetic components are included in the phenotypic values (Falconer, 1981). Therefore, when selecting eastern cottonwood families of the southern Great Plains for increasing diameter or height growth, indirect selection for increasing the number of branches per length of main stem will also take place.

CHAPTER V

SUMMARY OF RESULTS AND CONCLUSIONS

The southwestern portion of eastern cottonwood's native range was found to contain a large portion of genetic (stand and familywithin-stand) variation in many one and two year old nursery grown characters. For most of the characters the magnitude of the stand component of variance (as a percent of the total phenotypic variance) was at least 50 percent greater than the family-within-stand component. The extremely diverse environments of the study area have applied a diversity of selection pressures to its cottonwood population, resulting in observable differences among stands and geographic patterns of the differences. Differences among stand means were significant at the .05 probability level for greenhouse height (GHT), first and second year height (HT1 and HT2), first and second year date of leaf fall (LF1 and LF2), second year diameter (DIA), second year Melampsora leaf rust score (MLR) and second year number of branches per decimeter of main stem (BRPD) at each nursery and over nurseries.

Many characters also exhibited significant differences among family-within-stand means over locations, including height 1982 (HT1), diameter 1983 (DIA), date of leaf fall 1982 (LF1) and 1983 (LF2), Melampsora leaf rust score 1983 (MLR) and number of branches per decimeter 1983 (BRPD). Differences among greenhouse height family-

within-stand means were also significant. Significant differences among family-within-stand means for height 1983 (HT2) were found at the Broken Bow nursery but not at Norman or over nurseries.

Each character displayed a clinal pattern of geographic variation. A strong northwest-to-southeast pattern was found for growth rate characters (i.e. HT1, HT2 and DIA), with northwestern stands and families shorter in height and smaller in diameter than southeastern stands and families. However, a limit to seed movement along this trend was found, as extreme southeast Texas seedlings were growing slower than south Oklahoma seedlings at Norman. Provenance research with other wide-ranging forest tree species have also shown geographic limits to seedlot movement (Sprague and Wier, 1976; Ying and Bagley, 1976b; Bey, 1979).

Dates of leaf fall (LF1 and LF2) displayed a strong north-tosouth trend in variation, with northern stands and families reaching leaf fall earlier than southern stands and families. A lesser westto-east trend also existed, as western seedlings reached leaf fall earlier than eastern seedlings. The combination of these trends suggests a northwest-to-southeast pattern in variation for juvenile date of leaf fall, as was found for height and diameter characters. Mean number of frost free days was the most significantly correlated environmental factor with LF1 and LF2. Dates of leaf fall were earlier for seedlings originating from stands with shorter growing seasons (i.e. smaller mean number of frost free days).

A distinctive northwest-to-southeast pattern of variation was found for Melampsora leaf rust score 1983 (MLR), with northwestern stands and families having a higher percentage of infected leaf area than southeastern stands and families. The strength of this trend indicates that rust resistant genes can be introduced by utilizing planting stock which originates southeast of the proposed planting site.

A west-to-east geographic trend of decreasing number of branches per decimeter 1983 (BRPD) was found. In addition to being shorter in height and smaller in diameter, western stands and families produced more branches per unit length of main stem. Part of the distinction between the two eastern cottonwood varieties of this area (plains and eastern) may be differences in general tree form; the plains or western variety being short and branchy, while the eastern variety is tall and less branchy. Apparently the western conditions provide a selection advantage for conservative growth which results in short and branchy cottonwood seedlings, while liberal growth of cottonwood in eastern conditions results in tall and less branchy seedlings.

Location by stand interactions were significant for HT1, HT2, DIA, LF1, MLR, BRPD and SURV. For each character the difference in stand variances between locations were tested for significance, attempting to determine the source of the interaction. Significant differences in stand variances between locations for HT2, DIA, LF1,

LF2 and SURV were found. For these characters (HT1, DIA, LF1, LF2 and SURV) it appeared that a significant amount of the location by stand interaction was due to differences in stand variance between locations.

The location by family-within-stand interaction effect was significant for LF1. All other characters failed to exhibit a significant location by family interaction effect. The F-value for testing equal family-within-stand variances for LF1 between locations was not significant, which suggests that a change-in-rank type interaction occurred. This general lack in location by family-within-stand interaction effect is contrary to results obtained by Randall and Mohn (1969), Farmer (1970a) and Mohn and Randall (1973); however, these researchers studied location by clone interactions of eastern cottonwood.

Family mean narrow sense heritability estimates (h²) ranged from very low for percent survival (SURV), to low and medium for nursery growth characters (i.e. HT1, HT2 and DIA) and to medium and high for phenological and morphological characters (i.e. LF1, LF2 and BRPD) and Melampsora leaf rust score 1983. Extremely low heritability estimates for HT1 at Norman and at Broken Bow and for MLR at Norman were accompanied by very large standard errors, suggesting that these estimates may not be precise.

A simple mass selection program would appear to provide gains in date of leaf fall, Melampsora leaf rust resistance and number of

branches per length of main stem. The negative genetic correlation between LF2 and MLR ($r_{\rm G}$ = -.55) indicates that if selection was for later dates of leaf fall (based on LF2) a correlated decrease in MLR would accompany the increase in LF2. Progeny testing, over several locations, and family plus individual tree selection would be necessary to make reasonable gains in height and diameter. Selecting for taller height (based on HT2) would result in a correlated increase in diameter, date of leaf fall, Melampsora leaf rust infection and number of branches per length of main stem. Selecting for larger diameter (based on DIA) would result in a correlated increase in second year height, date of leaf fall, Melampsora leaf rust resistance and number of branches per decimeter.

The genetic correlation coefficients show strong and positive correlations for second year height with diameter, first year date of leaf fall with second year date of leaf fall and second year diameter with second year number of branches per decimeter. Strong and negative genetic correlations were found for greenhouse height with HT2 and LF2 with MLR. Height data on seven week old greenhouse grown seedlings does not appear to be useful as an early selection tool for increasing second year height. First year height was weakly and negatively correlated with second year height; however, this estimate was associated with a very large standard error.

The material utilized in this study has been outplanted at two field locations for further study and germplasm conservation. The

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LITERATURE CITED

- Barger, R.L. and P.L. Ffolliot. 1971. Prospects for cottonwood utilization in Arizona. Progressive Agriculture in Arizona 23:14-16.
- Bey, C.F. 1979. Geographic variation in <u>Juglans nigra</u> in the midwestern United States. Silvae Genetica 28:132-135.
- Brockman, C.F. 1968. Trees of North America. Golden Press, New York, 280 p.
- Cochran, W.G. and G.M. Cox. 1957. Experimental Designs. Second Edition. John Wiley and Sons, New York, 611 p.
- Cooper, D.T. and T.H. Filer, Jr. 1976. Geographic variation in Melampsora rust resistance in eastern cottonwood in the Lower Mississippi Valley. In: Proceedings of the 10th Central States Forest Tree Improvement Conference, p. 146-151, West Lafayette, IN.
- Crist, J.B., J.G. Isebrands and N.D. Nelson. 1979. Suitability of intensively grown <u>Populus</u> raw material for industry. In: Annual Meeting 1979 North American Poplar Council Proceedings, p. 65-72.
- Dhir, N.K. 1974. A comparative study of inter- and intra-provenance crosses of eastern cottonwood. Ph.D. Thesis, University of Minnesota, St. Paul, MN, 67 p.
- Dhir, N.K. and C.A. Mohn. 1976. A comparative study of crosses between and within two geographically diverse sources of eastern cottonwood. Canadian Journal of Forest Research 6:400-405.
- Eldridge, K.G., A.R. Route and J.W. Turnball. 1972. Provenance variation in the growth pattern of eastern cottonwood. Australian Forest Research 5:45-50.
- Falconer, D.S. 1981. Introduction to Quantitative Genetics. Second Edition. Longman, Inc., New York, 340 p.
- Farmer, R.E., Jr. 1966. Cottonwood improvement in the Lower Mississippi Valley. In: Proceedings of the Eighth Southern Conference on Forest Tree Improvement, p. 49-52, Savannah, GA.

- Farmer, R.E., Jr. 1970a. Variation and inheritance of eastern cottonwood growth and wood properties under two soil moisture regimes. Silvae Genetica 19:5-8.
- Farmer, R.E., Jr. 1970b. Genetic variation among open-pollinated progeny of eastern cottonwood. Silvae Genetica 19:149-151.
- Farmer, R.E., Jr. and J.R. Wilcox. 1965. Variation in juvenile growth and wood properties in half-sib cottonwood families. In: Joint Proceedings of the Second Genetics Workshop of the Society of American Foresters and the Seventh Lake States Forest Tree Improvement Conference, U.S.D.A. Forest Service Research Paper NC-6, p. 1-4, Northcentral Forest Experiment Station, St. Paul, MN.
- Farmer, R.E., Jr. and J.R. Wilcox. 1968. Preliminary testing of eastern cottonwood clones. Theoretical and Applied Genetics 38:197-201.
- Fowells, H.A. 1965. Silvics of Forest Trees of the United States. U.S.D.A. Forest Service Agriculture Handbook No. 271, Washington D.C., 762 p.
- Friend, M.M. 1981. Genetic variation in juvenile traits of eastern cottonwood from the southern United States. Unpublished M.S. Thesis, Mississippi State University, Starkville, MS, 114 p.
- Harlow, W.M., E.S. Harrar and F.M. White. 1979. Textbook of Dendrology. Sixth Edition. McGraw-Hill, Inc., New York, 510 p.
- Johnson, R.L. 1972. Genetically improved cottonwood--a research and development success. In: Proceedings of the National Convention of the Society of American Foresters, p. 113-119, Hot Springs, AR.
- Jokela, J.J. 1964. Breeding improved varieties of eastern cottonwood. Illinois Research, University of Illinois Agricultural Experiment Station, 6:6-7.
- Jokela, J.J., R.A. Melik and D.T. Cooper. 1982. Five-year results from the cottonwood evaluation plantation in southern Illinois. In: 19th Annual Meeting of the North American Poplar Council Proceedings, p. 69-73, Rhinelander, WI.
- Jokela, J.J. and C.A. Mohn. 1976. Geographic variation in eastern cottonwood. In: Proceedings of the Symposium on Eastern Cottonwood and Related Species, p. 109-125, Greenville, MS.

- Little, E.L., Jr. 1981. Forest Trees of Oklahoma. Oklahoma Forestry Division State Department of Agriculture, Oklahoma City, OK, 204 p.
- Lovett, W.R. 1979. The future of cottonwood in the central Great Plains. In: Annual Meeting 1979 of the North American Poplar Council Proceedings, p. 13-18.
- Lowe, W.R., R.W. Stonecypher and A.V. Hatcher. 1982. Progeny test data handling and analysis. In: Proceedings of the Workshop on Progeny Testing of Forest Trees. Southern Cooperative Series Bulletin No. 275, p. 51-66, Auburn, AL.
- Maisenhelder, L.C. 1970. Eastern cottonwood selections outgrow hybrids on southern sites. Journal of Forestry 68:300-301.
- Mohn, C.A. 1973. Practical breeding of cottonwood in the northcentral region. U.S.D.A. Forest Service General Technical Report NC-3 p. 35-39, Northcentral Forest Experiment Station, St. Paul, MN.
- Mohn, C.A. and S.S. Pauley. 1969. Early performance of cottonwood seed sources in Minnesota. University of Minnesota Forestry Research Note 207, St. Paul, MN, 4 p.
- Mohn, C.A. and W.K. Randall. 1969. Preliminary selection of eastern cottonwood clones. In: Proceedings of the 10th Southern Conference on Forest Tree Improvement, p. 41-48, Houston, TX.
- Mohn, C.A. and W.K. Randall. 1971. Inheritance and correlation of growth characters in <u>Populus</u> <u>deltoides</u>. Silvae Genetica 20: 182-184.
- Mohn, C.A. and W.K. Randall. 1973. Interaction of cottonwood clones with site and planting year. Canadian Journal of Forest Research 3:329-332.
- Muhle Larson, C. 1970. Recent advances in poplar breeding. International Review of Forestry Research, Academic Press, New York, 3:1-67.
- National Oceanic and Atmospheric Administration. 1974. Climate of the States, Volume II. United States Department of Commerce N.O.A.A., Water Information Center, Inc., 975 p.
- Pauley, S.S. 1949. Forest tree genetic research: <u>Populus</u> L. Economic Botany 3:299-330.

- Pauley, S.S. and T.O. Perry. 1954. Ecotypic variation of the photoperiodic response in <u>Populus</u>. Journal of the Arnold Arboretum 35:167-188.
- Posey, C.E. 1969. Phenotypic and genotypic variation in eastern cottonwood in the southern Great Plains. In: Proceedings of the 10th Southern Forest Tree Improvement Conference, p. 130-135, Houston, TX.
- Posey, C.E., F.E. Bridgewater and J.A. Buxton. 1969. Natural variation in specific gravity, fiber length and growth rate of eastern cottonwood in the southern Great Plains. Tappi 52: 1508-1511.
- Preston, R.J. 1976. North American Trees. Third Edition. Iowa State University Press, Ames, Iowa, 399 p.
- Randall, W.K. 1973. Mississippi cottonwoods outperform local clones near Cairo, Illinois. U.S.D.A. Forest Service Research Note SO-164, Southern Forest Experiment Station, New Orleans, LA, 3 p.
- Randall, W.K. and D.T. Cooper. 1973. Predicted genotypic gain from cottonwood clonal tests. Silvae Genetica 22:165-167.
- Randall, W.K. and C.A. Mohn. 1969. Clone-site interaction of eastern cottonwood. In: Proceedings of the 10th Southern Forest Tree Improvement Conference, p. 89-91, Houston, TX.
- Rockwood, D.L. 1968. Variation of eastern cottonwood along the course of the Mississippi River. Unpublished M.S. Thesis, University of Illinois, Urbana, IL, 50 p.
- SAS Institute Inc. 1982a. SAS User's Guide: Basics, 1982 Edition. SAS Institute Inc., Cary, NC, 923 p.
- SAS Institute Inc. 1982b. SAS User's Guide: Statistics, 1982 Edition. SAS Institute Inc., Cary, NC, 584 p.
- Schreiner, E.G. 1970. Genetics of eastern cottonwood. U.S.D.A. Forest Service Research Paper W0-11, 24 p.
- Sprague, J. and R. Wier. 1976. Geographic variation of sweetgum. In: Proceedings of the 12th Southern Conference on Forest Tree Improvement, p. 169-180, Baton Rouge, LA.
- Steel, R.G.D. and J.H. Torrie. 1980. Principals and Procedures of Statistics: A Biometrical Approach. Second Edition. McGraw-Hill Book Company, New York, 633 p.

- Stonecypher, R.W. 1969. Recurrent selection in forest tree breeding. In: Proceedings of the 10th Southern Conference on Forest Tree Improvement, p. 7-16, Houston, TX.
- Theilges, B.A. and J.C. Adams. 1975. Genetic variation and heritability of Mealmpsora rust resistance in eastern cottonwood. Forest Science 21:278-282.
- Walker, N. 1967. Growth and yield of cottonwood in central Oklahoma. Oklahoma State University Experiment Station Bulletin No. B-656, Stillwater, OK, 20 p.
- Wilcox, J.R. and R.E. Farmer, Jr. 1967. Variation and inheritance of juvenile characters of eastern cottonwood. Silvae Genetica 16:162-165.
- Wright, J.W. 1976. Introduction to Forest Genetics. Academic Press, Inc., New York, 463 p.
- Ying, C.C. 1974. Genetic variation in eastern cottonwood (<u>Populus</u> <u>deltoides</u> Bartr.) Department of Forestry University of Nebraska Progress Report No. 1, Lincoln, NE, 148 p.
- Ying, C.C. and W.T. Bagley. 1976a. Genetic variation of eastern cottonwood in an eastern Nebraska provenance study. Silvae Genetica 25:67-73.
- Ying, C.C. and W.T. Bagley. 1976b. Performance of green ash provenances of the Great Plains region. In: Proceedings of the 10th Central States Forest Tree Improvement Conference, p. 132-140, West Lafayette, IN.

APPENDIX A

STAND ORIGIN AND NURSERY SITE GEOGRAPHICAL

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AND ENVIRONMENTAL DATA

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TABLE XXV

Stand	State	County	Latitude (°North)	Longitude (°West)	River *
1	CO	Crowley	38° 25'	103° 45'	Arkansas
2	KS	Hamilton	37° 39'	101° 47'	Arkansas
3	KS	Ford	37° 46'	99° 58'	Arkansas
4	KS	Barton	38° 13'	98° 12'	Arkansas
5	KS	Cowley	37° 14'	96° 59'	Arkansas
6	KS	Cherokee	37° 10'	94° 50'	Neosho
7	OK	Cimarron	36° 44'	102° 30'	Cimarron
8	KS	Steward	37° 02'	100° 55'	Cimarron
9	OK	Woods	36° 46'	99° 07'	Cimarron
10	OK	Logan	35° 59'	97° 24'	Cimarron
11	OK	Tulsa	35° 57'	95° 50'	Arkansas
12	AR	Crawford	35° 20'	94° 22'	Arkansas
13	TX	Hutchinson	35° 34'	100° 57'	Canadian
14	OK.	Dewey	36° 02'	99° 30'	Canadian
15	OK	Canadian	35° 00'	98° 19'	Canadian
16	0K.	Hughes	35° 05'	96° 24'	Canadian
17	TX	Randall	34° 58'	102° 00'	Red (Prairie Dog Town Fork)
18	TX	Hall	34° 44'	100° 33'	Red (Prairie Dog Town Fork)
19	OK	Cotton	34° 10'	98° 00'	Red
20	OK	Love	33° 56'	97° 07'	Red
21	OK	Choctow	34° 00'	95° 24'	Red
22	AR	Miller	33° 27'	94° 00'	Red
23	TX	Garza	32° 40'	100° 50'	Brazos
24	TX	Haskell	33° 10'	99° 44'	Brazos
25	TX	Young	32° 45'	98° 04'	Brazos
26	TX	Dallas	32° 30'	96° 16'	Trinity
27	TX	Van Zandt	32° 40'	95° 30'	Neches

STAND ORIGIN GEOG	RAPHICAL D	ATA
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Stand	State	County	Latitude (°North)	Longitude (°West)	River *
28	TX	Coke	31° 54'	100° 29'	Colorado
29	TX	San Saba	31° 11'	98° 43'	Colorado
30	TX	Bosque	31° 36'	97° 13'	Brazos
31	TX	Leon	31° 47'	95° 39'	Trinity
33	TX	Llano	30° 45'	98° 41'	Guadalupe
34	TX	Travis	30° 18'	97° 42'	Colorado
35	TX	Brazos	30° 20'	96° 09'	Brazos
36	TX	Liberty	30° 03'	94° 48'	Trinity
38	TX	Gonzales	29° 30'	97° 27'	Guadalupe
39	TX	Wharton	29° 14'	96° 11'	Colorado
40	TX	Brazoria	29° 09'	95° 27'	Guadalupe
41	TX	Guadalupe	29° 40'	98° 07'	Brazos
42	TX	Victoria	28° 51'	96° 55'	Brazos

TABLE XXV (Continued)

* All stands were on the first flood plain. Soils were of alluvial origin and relatively deep.

Note: Data were taken from nearest recording station; therefore, some latitudes and longitudes may place stand in different county. Actual stand was within 15 miles of recording station.

Source: N.O.A.A., 1974.

TABLE XXVI

Stand	Mean ∦ Frost Free Days	Mean Annual Precipitation (cm)	Elevation (m)	Mean Annual Min. Temp. (°C)	L Mean Annual Max. Temp. (°C)
1	158	31.2	1173.5	-2	26
2	162	43.4	983.0	1	27
· 3	184	52.6	787.0	-6	28
4	187	72.6	498.7	-7	28
5	199	70.1	345.9	-6	29
6	198	88.1	275.8	-7	28
7	174	44.2	1268.0	4	26
8	183	41.9	865.6	-2	29
9	204	64.3	464.8	2	29
10	205	74.9	309.4	3	29
11	214	84.1	184.4	3	29
12	223	107.2	136.2	4	28
13	194	58.9	960.1	2	26
14	190	65.8	519.7	3	28
15	209	70.4	486.2	4	28
16	217	110.0	262.1	5	28
17	192	41.4	1094.2	4	26
18	211	58.4	640.1	2	28
19	218	92.5	266.7	6	30
20	227	108.7	257.6	6	29
21	222	118.6	142.0	6	28
22	227	125.0	119.2	1	28
23	204	49.8	711.7	1	29
24	226	40.1	489.2	1	29
25	213	69.9	284.7	2	30
26	239	99.6	128.0	2	30
27	244	101.3	129.5	1	29

STAND ORIGIN ENVIRONMENTAL DATA

.

Stand	Mean # Frost Free Days	Mean Annual Precipitation (cm)	Elevation (m)	Mean Annual Min. Temp. (°C)	Mean Annual Max. Temp. (°C)
28	212	42.9	542.5	3	29
29	227	65.8	364.2	2	29
30	247	68.6	150.9	3	30
31	246	102.4	182.9	4	29
33	228	64.5	317.3	5	31
34	260	81.5	182.0	5	30
35	280	98.0	65.5	4	29
36	259	129.8	10.7	6	28
38	266	83.3	95.1	6	30
39	266	100.6	32.0	8	28
40	288	134.1	8.2	7	27
41	251	83.3	216.4	6	31
42	305	89.4	31.7	8	29

TABLE XXVI (Continued)

Note: Data were taken from nearest recording station. Actual stand was within 15 miles of recording station.

Source: N.O.A.A., 1974.

TABLE XXVII

NURSERY SITE GEOGRAPHICAL AND ENVIRONMENTAL DATA

	Norman, OK	Broken Bow, OK
Latitude (°N)	35° 10'	34° 00'
Longitude (°W)	97° 25'	94° 35'
Mean # Frost Free Days	216	222
Mean Annual Precipitation (cm)	87.6	116 0
	07.0	116.8
Elevation (m)	350.5	262.1
Mean Annual Minimum Temperature (°C)	3	6
Mean Annual Maximum Temperature (°C)	28	28

Source: N.O.A.A., 1974.

APPENDIX B

GREENHOUSE, NURSERY, STAND AND FAMILY MEANS

TABLE XXVIII

FAMILIES SELECTED FOR USE IN THE GREENHOUSE AND NURSERY PHASES, BASED ON GERMINATION PERCENT AND THE PERCENT GERMINATION OBSERVED FOR THOSE FAMILIES

Stand- Family	Percent Germination	Stand- Family	Percent Germination	Stand- Family	Percent Germination
1-2	84	8-1	86	15-2	78
1-3	96	8-2	78	15-3	90
1-4	70	8-3	67	15-4	90
1-5	84	8-5	56	15-5	86
2-1	86	9-1	86	16-1	88
2-2	84	9-2	76	16-2	68
2-3	90	9-4	96	16-4	78
2-4	92	9-5	86	16-5	72
3-1	92	10-2	12	17-1	
3-2	76	10-3	86	17-2	96
3-4	84	10-4	40	17-3	88
3-5	76	10-5	60 -	17-4	80
4-1	88	11-1	78	18-2	58
4-2	100	11-3	94	18-3	96
4-3	96	11-4	94	18-4	96
4-5	92	11-5	90	18-5	67
5-1	90	12-1	42	19-1	92
5-2	88	12-3	76	19-2	72
5-3	54	12-4	62	19-3	70
5-4	84	12-5	92	19-4	80
6-1	65	13-1	72	20-2	70
6-2	70	13-2	88	20-3	84
6-3	68	13-4	90	20-4	72
6-4	86	13-5	84	20-5	74
7-2	76	14-1	84	21-1	88
7-3	72	14-2	92	21-2	68
7-4	80	14-3	90	21-4	78
7-5	94	14-4	70	21-5	72

Stand-	Percent	Stand-	Percent	Stand -	Percent
Family	Germination	Family	Germination	Family	Germination
22-2	40	28-1	76	36-1	32
22-3	56	28-3	98	36-2	14
22-4	50	28-4	48	36-3	12
22-5	56	28-5	70	36-4	24
23-2	96	29-1	62	38-1	34
23-3	36	29-2	88	38-2	40
23-4	36	29-4	72	38-3	24
23-5	??	29-5	74	38-5	66
24-2	62	30-1	90	39–1	52
24-3	70	30-3	78	39–3	56
24-4	88	30-4	78	39–4	46
24-5	82	30-5	68	39–5	48
25-1	98	31-1	46	40-1	48
25-2	72	31-2	38	40-2	28
25-3	84	31-3	72	40-3	62
25-5	86	31-4	56	40-4	38
26-1 26-2 26-3 26-5	20 86 86 82	33-1 33-3 33-4 33-5	68 72 46 88	41-1 41-2 41-4	38 10 78
27-1	65	34-1	90	42-1	32
27-2	53	34-3	62	42-2	22
27-4	74	34-4	60	42-4	40
27-5	52	34-5	84	42-5	80
		35-1 35-2 35-3 35-4	30 56 52 50		

TABLE XXVIII (Continued)

TABLE XXIX

POOLED NURSERY AND GREENHOUSE HEIGHT MEANS WITH STANDARD ERRORS

Character	Number of Observations	Mean	Standard Error of the Mean
Height 1982	5039	25.3 cm	0.15
Height 1983	4595	205.8 cm	0.97
Diameter 1983	4594	14.9 mm	0.09
Date of Leaf Fall 1982	5125	31 days*	0.2
Date of Leaf Fall 1983	4583	25 days**	0.2
Melampsora Leaf Rust Score 1983	4576	30%	0.4
Number of Branches per Decimeter 1983	4594	0.87	0.008
Greenhouse Height August 24, 1982	6190	9.62 cm	0.045
Survival 1983	<i>x</i>	73.3%	

Note: * number of days past November 1, 1982 ** number of days past October 31, 1983

TABLE XXX

Character	Number of Observations	Mean	Standard Error of the Mean
NORMAN NURSERY			
Height 1982	2645	27.4 cm	0.22
Height 1983	2468	223.5 cm	1.31
Diameter 1983	2467	16.1 mm	0.11
Date of Leaf Fall 1982	2461	38 days*	0.2
Date of Leaf Fall 1983	2450	30 days**	0.3
Melampsora Leaf Rust Score 1983	2455	29%	0.6
Number of Branches per Decimeter 1983	2468	1.07	0.010
Survival 1983		79.4%	
BROKEN BOW NURSERY			
Height 1982	2394	23.0 cm	0.20
Height 1983	2127	185.4 cm	1.31
Diameter 1983	2127	13.5 mm	0.12
Date of Leaf Fall 1982	2484	24 days*	0.3
Date of Leaf Fall 1983	2133	20 days**	0.1
Melampsora Leaf Rust Score 1983	2121	31%	0.5
Number of Branches per Decimeter 1983	2126	0.64	0.010
Survival 1983		67.5%	

NORMAN AND BROKEN BOW NURSERY MEANS WITH STANDARD ERRORS

Note: * number of days past November 1, 1982 ** number of days past October 31, 1983

TABLE XXXI

HIGHEST AND LOWEST FIVE RANKING POOLED STAND MEANS WITH STANDARD ERRORS FOR GHT, HT1, HT2 AND DIA

	G] (HT cm)	H'	rl cm)	H	HT2 (cm)	D) (1	IA mm)
RANK	Stand	X±se	Stand	X±se	Stand	l X±se	Stand	X±se
1	23	12.6±0.3	40	32.9±0.1	21	245.9±5.9	34	18.5±0.6
2	.4	11.5±0.3	34	32.5±1.1	34	238.5±5.8	21	18.3±0.6
3	5	11.2±0.3	39	32.5±1.1	39	229.8±5.6	36	17.3±0.7
4	3	11.1±0.3	31	32.0±1.2	20	226.2±6.0	38	17.2±0.5
5	9	11.0±0.3	38	31.8±1.2	11	225.6±5.5	40	17.2±0.6
•								
•								
•	35	8.6±0.3	,			1		
36	29	8.6±0.3	4	20.5±0.6	3	168.0±5.0	13	11.1±0.4
37	26	8.4±0.2	7	19.5±0.7	17	165.7±4.7	17	11.0±0.4
38	33	7.8±0.3	3	19.3±0.6	7	162.4±5.4	7	10.7±0.4
39	22	7.4±0.2	2	17.0±0.5	2	149.6±4.3	1	9.8±0.4
40	36	6.5±0.3	1	16.9±0.6	1	146.7±5.6	2	9.7±0.3

TABLE XXXII

HIGHEST AND LOWEST FIVE RAN	KING POOLED
STAND MEANS WITH STANDAR	D ERRORS
FOR LF1, LF2, MLR AND	BRPD

	L da ⁻	F1 ys*)	L (da	F2 ys * *)	MI (%)	LR)		BRPD
RANK	Stand	X±se	Stand	X±se	Stand	X±se	Sta	nd X±se
1	39	43±1	36	39±1	2	66±2	18	1.37±0.06
2	40	42±1	39	39±1	1	64±2	19	1.20±0.06
3	42	41±1	40	37±1	8	61±3	14	1.16±0.06
4	36	41±1	42	36±1	7	56±3	5	1.05±0.05
5	41	40±1	35	35±1	3	55±2	24	1.01±0.06
•	35	40±1						
•								
•	4	22±1						
36	7	22±1	17	16±1	40	13±1	35	0.69±0.04
37	8	21±1	7	16±1	34	12±1	6	0.68±0.04
38	3	20±1	1	15±1	39	11±1	1	0.67±0.05
39	1	18±1	8	14±1	22	8±1	21	0.57±0.03
40	2	18±1	3	14±1	36	6±1	12	0.52±0.04

Note: * number of days past November 1, 1982

** number of days past October 31, 1983

TABLE XXXIII

HIGHEST AND LOWEST FIVE RANKING NORMAN STAND MEANS WITH STANDARD ERRORS FOR HT1, HT2 AND DIA

	H. (([1 cm)	F (HT2 (cm)	DIA (mm)		
RANK	Stand	X±se	Stand	X±se	Stand	X±se	
1	31	37.8±1.7	21	271.8±9.6	21	20.0±0.9	
2	34	37.2±1.7	12	262.7±7.7	34	19.4±0.7	
3	39	34.7±1.7	20	255.1±7.8	20	18.8±0.7	
4	38	34.7±1.6	34	253.4±7.8	22	18.4±0.9	
5	40	34.4±1.7	19	251.1±9.7	38	18.2±0.6	
•					11	18.2±0.7	
•							
•							
36	7	22.1±0.9	18	186.3±7.4	13	13.1±0.4	
37	18	21.7±1.0	7	184.0±5.4	17	12.5±0.4	
38	3	19.9±0.7	17	183.6±5.2	7	12.5±0.4	
39	1	18.3±0.8	1	171.0±5.4	1	11.5±0.4	
40	2	16.9±0.6	2	170.1±4.7	2	11.1±0.4	

TABLE XXXIV

HIGHEST AND LOWEST FIVE RANKING NORMAN STAND MEANS WITH STANDARD ERRORS FOR LF1, LF2, MLR AND BRPD

RANK	LF1 (days*) Stand X+aa		LF2 (days	LF2 (days**)		MLR (%)		BRPD
		Arse	Scand	AISE	Stand	X±se	Stan	d X±se
1	40	49±1	39	42±1	1	65±3	19	1.54±.07
2	42	46±2	36	41±1	2	63±3	18	1.48±.07
3	33	45±2	40	40±1	7	56±4	14	1.39±.06
4	41	45±1	19	40±1	17	54±4	5	1.27±.05
5	39	44±1	42	39±1	3	53±3	23	1.25±.06
•	23	44±2	34	39±1	8	53±4		
•								
•		,						
36	7	31±1	17	21±2	6	13±2	6	0.87±.06
37	2	31±1	8	21±2	36	10±2	35	0.81±.06
38	6	29±1	1	21±2	34	10±2	36	0.77±.04
39	1	29±1	7	20±2	30	9±2	21	0.73±.05
40	3	28±1	3	19±2	22	8±2	12	0.72±.05

Note: * number of days past November 1, 1982

** number of days past October 31, 1983

TABLE XXXV

	H1 (c	F1 cm)]	HT2 (cm)	DIA (mm)		
RANK	Stand	- X±se	Stand	X±se	Stand	X±se	
1	40	31.2±1.1	35	230.6±6.9	36	18.8±1.2	
2	39	30.2±1.5	39	227.8±6.5	34	17.6±0.9	
3	38	28.3±1.3	21	224.2±6.2	39	17.5±0.7	
4	42	28.3±1.2	34	222.1±8.2	41	17.1±0.7	
5	34	27.9±1.3	36	212.0±9.7	35	17.0±0.7	
•							
•							
•							
36	3	18.4±1.0	13	131.7±6.7	13	7.9±0.5	
37	2	17.0±0.7	17	128.4±5.5	17	7.9±0.4	
38	5	16.9±1.0	2	117.5±4.8	2	7.5±0.4	
39	7	16.6±0.8	7	117.2±7.1	7	7.0±0.4	
40	1	15.3±0.8	1	94.8±6.3	1	6.1±0.5	

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HIGHEST AND LOWEST FIVE RANKING BROKEN BOW STAND MEANS WITH STANDARD ERRORS FOR HT1, HT2 AND DIA

,

TABLE XXXVI

	LF (day	71 vs*)	LF: (days	2 s**)	ML: (%)	R)	BRI	PD
RANK	Stand	<u> </u>	Stand	<u> X</u> ±se	Stand	X±se	Stand	X±se
1	39	41±2	36	38±1	2	71±3	18	1.18±.10
2	36	40±2	39	36±1	8	69±3	19	0.93±.08
3	35	37±1	40	35±1	4	62±2	33	0.87±.06
4	42	36±2	35	33±1	1	60±4	41	0.87±.06
5	40	36±1	42	33±1	3	59±3	38	0.87±.06
•								
•				,				
•								
•	4	11±1	8	7±1				
36	7	11±1	7	7±1	35	11±1	21	0.44±.04
37	3	10±1	3	7±1	39	9±1	17	0.41±.06
38	8	9±1	17	5±1	40	8±1	12	0.33±.03
39	1	7±1	1	4±1	22	8±1	7	0.29±.06
40	2	5±1	2	3±1	36	2±1	1	0.25±.07

HIGHEST AND LOWEST FIVE RANKING BROKEN BOW STAND MEANS WITH STANDARD ERRORS FOR LF1, LF2, MLR AND BRPD

Note: * number of days past November 1, 1982

** number of days past October 31, 1983

TABLE XXXVII

	No	rman	Broke	en Bow	Pooled		
RANK	Stand	Survival 1983 (%)	Stand	Survival 1983 (%)	Stand	Survival 1983 (%)	
1	18	91.3	41	88.3	39	87.5	
2	17	90.8	39	87.5	40	84.4	
3	13	90.0	40	86.3	41	82.5	
4	31	88.5	22	82.5	22	80.4	
5	39	87.5	6	80.0	20	79.4	
•							
•							
•							
36	36	71.9	5	53.8	28	68.6	
37	8	70.0	2	48.7	17	65.4	
38	26	67.1	17	41.3	2	60.9	
39	21	65.0	. 1	36.3	7	57.7	
40	19	63.2	7	36.3	1	57.6	

HIGHEST AND LOWEST FIVE RANKING STAND MEANS FOR PERCENT SURVIVAL 1983

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TABLE XXXVIII

HIGHEST AND LOWEST SEVEN RANKING POOLED FAMILY MEANS WITH STANDARD ERRORS FOR GHT, HT1, HT2 AND DIA

	GHT (cm)		HT1 (cm)		HT (c	2 m)	DIA (mm)	
RANK	ST-F	X±se	ST-F		ST-F		ST-F	X±se
1	23-4	14.8±.5	34-4	39.8±2.7	21-4	259.6±10.2	21-4	20.9±1.2
2	4-5	12.8±.5	38-3	38.4±2.3	16-5	253.0±14.7	34-5	20.5±1.5
3	23-5	12.6±.8	38-1	36.2±2.0	34-4	249.1±13.4	33-4	19.5±0.9
4	34-4	12.4±.7	39-4	35.9±1.9	21-2	247.4±13.6	40-2	19.2±1.2
5	4-3	12.3±.8	40-4	35.6±2.0	33-4	247.0± 9.5	36-4	19.1±1.3
6	10-4	12.1±.7	31-3	35.4±2.6	12-4	246.4±13.5	22-5	19.1±0.9
7	40-4	12.1±.6	31-4	33.9±2.3	19-4	244.4±11.0	34-4	19.0±1.3
•								
•								
•								
153	33-3	7.3±.4	3-1	17.5±0.8	3-4	150.5±10.5	13-2	10.1±0.8
154	22-5	7.0±.4	2-2	16.7±0.7	2-1	149.0± 6.9	18-3	10.0±0.8
155	10-2	6.8±.5	2-5	16.6±1.1	18-3	144.0± 6.9	2-5	9.8±0.7
156	22-4	6.7±.3	1-5	16.0±0.9	14-2	143.1± 8.4	2-1	9.8±0.7
157	36-4	6.7±.5	7-5	15.7±1.2	1-5	141.3± 8.2	1-5	9.3±0.5
158	36-3	6.1±.5	2-1	15.7±0.9	2-2	133.3± 6.2	2-2	8.9±0.4
159	36-2	4.6±.8	1-3	14.2±1.0	1-3	122.1± 8.9	1-3	8.2±0.7

Note: ST-F Stand#-Family(within stand)#

TABLE XXXIX

LF1 (days*		1 s*)	LF: (day:	2 s**)	ML] (%)	R)	BRF	D
RANK	ST-F	X ±se	ST-F	αse	ST-F	Χ±se	ST-F	<u>X</u> ±se
1	39–5	47±2	36-1	42±1	2-2	72±3	18-2	1.68±.10
2	41-2	47±2	39–4	40±1	2-1	69±4	14-1	1.57±.09
3	42-4	45±3	40-4	40±2	1-2	69±6	24-4	1.44±.10
4	36-4	45±1	42-4	40±2	3-5	68±4	19-4	1.43±.10
5	40-3	44±3	41-2	40±1	1-5	68±5	16-1	1.42±.08
6	42-2	43±3	а	39	8-2	67±4	18-4	1.40±.11
7	40-4	43±2			7-5	67±3	18-5	1.37±.09
•	39-1	43±1		`				
•								
•								
•					-			
153	1-5	18±3			22-4	6±2	40-3	0.55±.06
154	2-5	18±3			36-1	6±2	1-3	0.53±.09
155	4-1	18±3			22-2	5±2	1-5	0.50±.08
156	8-5	18±3	Ъ	13	29-2	5±2	35-3	0.49±.05
157	1-3	17±2	3-1	12±2	39-4	4±1	21-5	0.43±.05
158	2-2	16±3	8-5	11±3	36-4	4±2	21-3	0.42±.06
159	7-5	15±2	1-5	10±2	22-5	4±2	12-3	0.38±.04

HIGHEST AND LOWEST SEVEN RANKING POOLED FAMILY MEANS WITH STANDARD ERRORS FOR LF1, LF2, MLR AND BRPD

Note:	ST-F	Stand#-Family(within stand)#
	*	number of days past November 1, 1982
~	**	number of days past October 31, 1983
	а	five families tied at 39 days
	Ъ	seven families tied at 13 days

TABLE XL

	H' (-	T1 cm)	H' (*	T2 . cm)	D) (1	IA nm)	
RANK	ST-F	X±se	ST-F	X±se	ST-F		
1	34-4	49.9±3.2	16-5	293.1±17.4	20-1	22.1±1.7	
2	31-3	43.0±2.7	21-2	292.8±16.4	21-2	22.0±1.6	
3	38-1	41.0±3.2	28-5	290.3±13.2	34-4	21.9±1.4	
4	31-4	40.9±3.1	30-1	284.5±15.7	11-5	21.6±1.0	
5	38-3	40.4±3.4	34-4	283.4±10.7	40-2	21.5±1.8	
6	40-4	39.8±2.2	21-3	282.4±19.2	33-4	20.8±1.1	
7	34-1	39.0±2.3	20-5	278.1±12.7	16-5	20.6±1.3	
•							
•							
•			,				
153	3-1	18.1±1.1	4-2	170.3±14.2	33-5	11.4±1.2	
154	4-2	17.5±1.5	2-5	167.2± 9.0	2-5	10.8±0.7	
155	1-5	16.7±1.2	1-5	162.2± 8.1	18-3	10.8±1.1	
156	2-5	16.4±1.4	18-3	153.5±15.5	1-5	10.8±0.5	
157	2-1	15.3±1.3	2-2	148.8± 7.4	14-2	10.7±0.8	
158	2-2	15.2±1.2	14-2	142.8± 9.4	2-2	10.0±0.5	
159	1-3	14.1±1.1	1-3	141.0± 9.3	1-3	9.5±0.8	

HIGHEST AND LOWEST SEVEN RANKING NORMAN FAMILY MEANS WITH STANDARD ERRORS FOR HT1, HT2 AND DIA

Note: ST-F Stand#-Family(within stand)#

TABLE XLI

	L] (dav	Fl vs*)	L] (day	F2 ys**)	M	LR %)	I	BRPD
RANK	ST-F	X±se	ST-F	<u>X</u> ±se	ST-F	X±se	ST-F	
1	40-3	56±3	36-1	44±1	1-5	72±7	18-2	1.91±.09
2	23-5	53±3	41-2	44±1	3-5	71±5	19-4	1.79±.09
3	42-4	52±4	39-1	44±1	3-3	70±5	14-1	1.68±.10
4	35-4	51±3	42-4	43±3	1-2	68±6	24-4	1.65±.11
5	39-5	50±3	34-4	43±2	2-1	68±7	19-2	1.64±.13
6	33-4	50±3	b	42	1-3	68±6	8-3	1.57±.11
7	41-2	50±3	,		7-5	67±3	14-4	1.55±.10
•	33-1	50±4	ĸ					
•								
•				a a				
•				* . *	30-4	7±3	1-3	0.71±.10
•					25-1	7±3	21-3	0.71±.04
153	а	28	17-1	17±2	22-2	7±3	12-5	0.71±.10
154	1-3	26±2	6-4	17±3	21-3	6±3	1-5	0.70±.09
155	7-3	26±1	3-1	16±3	12-1	6±3	20-3	0.69±.08
156	1-2	25±1	1-3	16±3	26-1	5±3	36-1	0.64±.06
157	7-5	24±2	3-5	16±3	22-5	2±2	35-3	0.56±.08
158	3-5	24±2	1-5	15±3	22-4	1±1	12-3	0.55±.05
159	6-3	21±4	7-3	14±2	29-2	1±1	21-5	0.48±.07

HIGHEST AND LOWEST SEVEN RANKING NORMAN FAMILY MEANS WITH STANDARD ERRORS FOR LF1, LF2, MLR AND BRPD

Note: ST-F Stand#-Family(within stand)#

* number of days past November 1, 1982

** number of days past October 31, 1983

a four families tied at 28 days

b nine families tied at 42 days

TABLE XLII

	F (HT1 (cm)		HT2 (cm)	DIA (mm)		
RANK	ST-F	X±se	ST-F	X±se	ST-F	X±se	
1	38-3	35.7±3.0	21-4	271.3±10.3	21-4	22.3±1.4	
2	35-1	34.9±2.4	35-1	247.7± 8.3	34-5	20.9±2.7	
3	39-4	32.7±2.3	39-4	241.0±11.5	39-4	19.9±1.5	
4	40-1	32.5±1.7	35-4	234.4±13.7	36-4	19.6±2.2	
5	39-5	32.3±3.4	38-2	231.1± 9.4	36-2	19.0±2.2	
6	34-4	32.0±3.1	39-3	230.5±11.0	36-3	18.7±2.0	
7	39-3	31.8±2.5	39-5	230.3±12.1	40-4	18.6±2.4	
•	40-4	31.8±2.9					
•							
•							
•	2-1	15.5±1.2					
153	36-2	15.5±3.8	1-5	106.4± 9.2	13-2	6.7±0.8	
154	1-5	15.4±1.3	2-4	101.6±14.5	2-4	6.3±1.1	
155	4-5	14.7±1.9	7-4	97.8±12.7	1-3	6.3±1.1	
156	1-2	14.4±1.3	1-3	94.7±13.9	7-4	6.0±0.7	
157	1-3	14.2±1.6	7-3	87.0±13.0	1-2	5.6±	
158	5-2	12.5±1.7	1-2	83.8±	1-4	5.2±0.4	
159	7-5	11.9±1.6	1-4	83.2± 6.8	7-3	5.0±0.8	

HIGHEST AND LOWEST SEVEN RANKING BROKEN BOW FAMILY MEANS WITH STANDARD ERRORS FOR HT1, HT2 AND DIA

Note: ST-F Stand#-Family(within stand)#

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TABLE XLIII

	LF1 (days*)		LF2 (days**)		MLR (%)		BRPD	
RANK	ST-F	X±se	ST-F	X±se	ST-F	X±se	ST-F	X±se
1	36-4	47±2	36-2	41±1	8-5	83±7	16-1	1.40±.08
2	39-1	47±2	40-4	40±1	1-4	83±5	14-1	1.38±.18
3	41-2	44±3	36-1	39±2	1-2	80±-	18-2	1.34±.16
4	39-5	43±2	36-4	39±1	8-2	77±5	18-5	1.26±.14
5	35-2	41±4	39-4	39±1	2-2	75±4	24-4	1.22±.14
6	21-4	41±4	42-4	38±2	4-5	73±8	18-3	1.21±.29
7	40-1	40±3	39-3	37±2	17-3	73±5	41-2	1.17±.11
•	42-4	40±3	39-5	37±1				
•			*					
•								,
153			2-1	3±1	36-3	4±3	12-3	0.23±.04
154			13-2	3±1	36-1	4±2	7-4	0.23±.05
155	a	6	2-2	2±0	22-2	3±2	7-5	0.21±.08
156	8-5	5±2	8-5	2±0	38-2	2±2	3-4	0.18±.07
157	2-4	5±3	1-4	1±0	36-4	1±1	1-5	0.16±.07
158	7-5	3±1	1-5	1±0	39-4	1±1	1-2	0.12±
159	2-2	2±1	1-2	1±-	36-2	0±0	7-3	0.10±.06

HIGHEST AND LOWEST SEVEN RANKING BROKEN BOW FAMILY MEANS WITH STANDARD ERRORS FOR LF1, LF2, MLR AND BRPD

Note: ST-F Stand#-Family(within stand)#

* number of days past November 1, 1982

** number of days past October 31, 1983

a six families tied at 6 days
TABLE XLIV

	Norman		Broken Bow		Pooled	
RANK	Stand- Famíly	Survival 1983 (%)	Stand- Family	Survival 1983 (%)	Stand- Family	Survival 1983 (%)
1	42-5	100.0	40-1	100.0	39-4	97.5
2	27-1	100.0	39-4	100.0	40-1	95.0
3	17-4	100.0	41-4	95.0	22-5	92.5
4	5-1	100.0	39-3	95.0	39-5	90.0
5	а	95.0	30-1	95.0	d	87.5
6			9-1	94.7		
7			с	90.0		
•						
•						
•						
153	b	60.0	2-5	31.3	7-5	58.3
154	36-3	57.9	17-1	30.0	36-3	56.8
155	30-1	50.0	7-5	30.0	17-1	55.3
156	21-3	50.0	4-5	30.0	2-4	55.0
157	19-1	50.0	2-4	25.0	2-5	50.0
158	6-3	50.0	7-3	20.0	7-3	42.5
159	42-4	45.0	1-1	5.0	1-1	42.1

HIGHEST AND LOWEST SEVEN RANKING FAMILY MEANS FOR PERCENT SURVIVAL 1983

Note: a 12 families tied at 95.0%

b six families tied at 60.0%

c five families tied at 90.0%

d six families tied at 87.5%

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FAMILY-PLOT MEANS

FREQUENCY HISTOGRAMS OF POOLED LOCATIONS

APPENDIX C



Figure 17. Frequency Histogram of Greenhouse Height (GHT) Family-Plot Means



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Figure 18. Frequency Histogram of Height 1982 (HT1) Family-Plot Means

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Figure 19. Frequency Histogram of Height 1983 (HT2) Family-Plot Means



Figure 20. Frequency Histogram of Diameter 1983 (DIA) Family-Plot Means



Figure 21. Frequency Histogram of Date of Leaf Fall 1982 (LF1) Family-Plot Means



Figure 22. Frequency Histogram of Date of Leaf Fall 1983 (LF2) Family-Plot Means



Figure 23. Frequency Histogram of Melampsora Leaf Rust Score 1983 (MLR) Family-Plot Means

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Figure 24. Frequency Histogram of Number of Branches per Decimeter 1983 (BRPD) Family-Plot Means



Figure 25. Frequency Histogram of Percent Survival 1983 (SURV) Family-Plot Means

APPENDIX D

STANDARD ERROR OF HERITABILITY AND OF GENETIC

CORRELATION COEFFICIENT FORMULAE

.

se(E) =
$$\left[\sum (dE / dM_{ij})^2 (Mij^2 + M_iM_j / k_{ij})\right]^{\frac{1}{2}}$$

Note: dE / dM_{ij} = derivative of E with respect to M_{ij} E = expression for the estimate of interest (h² or r_{GXY}) M_i = ith mean square M_j = jth mean square M_{ij} = i X j mean cross-product if i = j the M_{ij} = M_i and M_{ij}² + M_iM_j = 2(M_i)² k_i = degrees of freedom associated with the ith mean square k_{ij} = degrees of freedom associated with the i X j mean cross-product

if i = j then $k_{ij} = k_i$

Figure 26. Standard Error Formula

VITA²

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Master of Science

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