Genetic Variation of Eastern Cottonwood in an Eastern Nebraska Provenance Study[1])

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Introduction

There is an increasing need for trees to produce wood and to provide protection and aesthetic amenties. Attention is focused on multipurpose trees capable of rapid growth and tailored to specific site conditions. Populus species have been cultivated widely throughout the world and meet these requirements remarkably well.

Eastern cottonwood (Populus deltoides BARTR.) is a native dioecious species of a wide area of the Eastern United States and has been planted throughout the world. Rapid growth, ease of vegetative propagation, wide range of genetic variation, compatibility in intra- and inter-species hybridization, and short regeneration cycles make eastern cottonwood a prime candidate for genetic improvement and suitable experimental material for basic genetic investigations of tree species.

Genetic and breeding research of poplars was reviewed by PAULEY (1949) and more recently by MUHLE LARSEN (1970) and SCHREINER (1970). Since most genetic studies have dealt with local populations, information of rangewide geographic variation is still lacking.

A range-wide provenance test of eastern cottonwood was esablished near Mead, Nebraska, in 1966 as a part of a regional tree improvement project of the North Central State Agricultural Experiment Stations (NC-99). The Department of Forestry, University of Illinois, provided leadership in seed collection and grew and distributed the nursery stock. This report evaluates the performance of clones during the first seven years of the Nebraska planting and attempts to determine the pattern of genetic diversity and the interrelationship of morphological, phenological, and growth characteristics of this species.

Materials and Methods

A provenance plantation of 498 clones of eastern cottonwood (Populus deltoides BARTR. derived from 116 open-pollinated families was established by planting unrooted cuttings in 1966 near Mead in eastern Nebraska, at 40 degrees latitude (Figure 1). Number of clones in each family ranged from 1 to 6. Twenty clones of two families of Populus *nigra* of Italian origin were also included. Clones within the planting were completely randomized with three replications of single tree plots. The planting site was on level bottom land of colo silty clay loam soil susceptible to occasional flooding. Spacing was 5 meters between rows and 3.4 meters within rows. The plantations occupies 2.2 hectares. Dead trees were replaced in 1967. All trees were pruned to a single stem in 1967.

Height was measured annually. Diameters were recorded annually since 1970. Phenological data included dates of leaf flush and anthesis in 1973 and 1974.

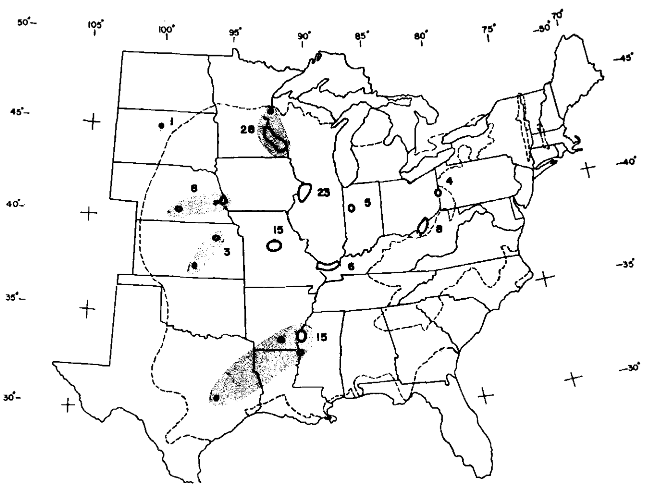

Figure 1. — Natural range of P. *deltoides* BAHTR. is bounded by dashed line. Locations of seed trees are represented by circled areas. Several collections were combined into one provenance (shaded). Numeral indicates number of seed trees. *plantation location.

Five leaves were measured from one ramet of each of 156 clones. Leaves were collected from terminal or collateral shoots of the current year's growth about 15 feet above ground. Samples were limited to the fourth to the ninth of the early leaves to minimize within-tree variation (CRITCHFIELD 1960). Catkin and capsule characteristics of 82 clones were measured.

Bark thickness was measured and roughness noted using a scale of 1 to 4 as illustrated in Figure 2. Stem form of trees was rated on a scale of 1 to 4, ranging from straight to forked near the ground. Branching habit was rated from 1 to 4 (Figure 3). The last three characteristics were measured on trees taller than 8 meters.

All families were grouped into 11 provenances (*Figure* 1). Variance analyses were based on hierarchial design of provenance, family (maternal parent) within provenance and clone within family. Combined analyses were performed on characteristics evaluated in more than one year. Analyses assume homogeneous variance of all provenances and random parent trees.

Approxirnate between-provenance LSDs were calculated to differentiate provenance means.

$$LSD = \left(\frac{\text{Mean square of family means}}{\text{coefficient of variance component of provenance mean}}\right)^{\frac{1}{2}}$$

multiplied by Duncan's range difference of the 1 or 5 percent level. Simple correlations between progeny traits and latitude and longitude of seed origin and among progeny traits were computed using family means as items.

Results and Discussion

Injury, Diseuse *and* Mortality The average survival for the plantation was 91% with several sources averaging 85

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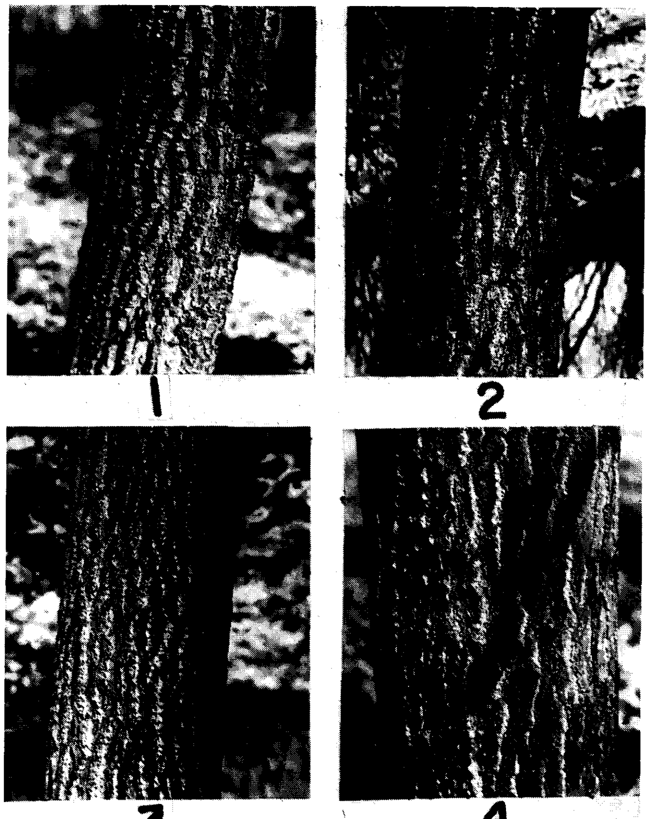

Figure 2. — Bark character. Numbers refer to bark roughness scores (1 — very rough, 2 — rough, 3 — medium, 4 — smooth). Rough bark was typical of trees of eastern provenances and smoother bark was found on most trees of western and northern origin

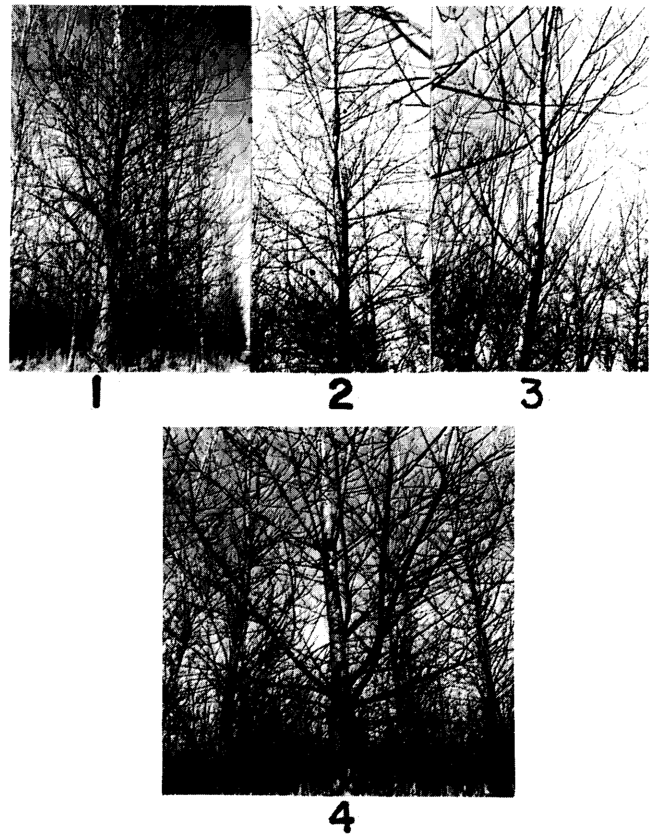

Figure 3. — Branching habit showing the range from small short side branches typical of trees of Minnesota-Wisconsin and other western provenances to few large long branches most common among trees of eastern provenances.

to 100% living. The best survival was in northern provenances with the exception of the South Dakota source with only 70% living. Winter injury and mortality were very high among progenies from Mississippi, Arkansas and Texas (south of 33 degrees latitude) with 41% dead and 50 percent suffering dieback from the branch tips in varying amounts during two or more winters. Sixty percent of trees of Southern Illinois origin survived. Because trees from these southern areas retained their leaves late into the growing season, winter injury can be attributed to the presence of succulent tissues at the time of the first sharp freeze in autumn.

The greatest dieback was noticed in 1970 when height measurements at the end of that growing season showed no or little increase from the year previous on many trees of southern origin. Clones with tendencies to grow late into the autumn were probably injured by a mid-October freeze .

By 1973, stem canker among trees of South Dakota origin was as prevalent as it was among the *P. nigra* clones in the planting. "Siouxland", a selected clone resistant to leaf rust from South Dakota, has been reported as very susceptible to stem canker disease (BAGLEY 1973).

Growth Height and diameter growth were influenced by provenance, family and clone *(Table 1)*. Relative value of variance components of provenance, family, and clone increased, accompanied by the decrease of error components as age of the plantation increased *(Figure 2)*. This indicates that genetic factors become more dominant in determining rate of growth than site factors as the trees grow older. However, the relatively large ramet/clone variation suggests that height growth of cottonwood clones is sensitive to the effect of microsite. A large number of replications would be necessary to evaluate genotypic value of individual clones in growth rate.

Table 1. — Estimates of variance components for growth, stem form, and bark character, expressed as percent of the total variation.

Source of Variation	DF	Height Age 7	DBH Age 7	DBH Height Ratio	DF	Bark Roughness	DF	Bark Thickness	Stem Form
Provenances	10	10*	8*	7*	10	37*	10	31*	10*
Families/P	100	8*	9*	7*	97	11*	93	8*	8*
Clones/F	362	12*	11*	14*	355	23*	323	22*	12*
Ramets/C	773	70	72	71	709	29	532	38	70

* Variance ratio from variance analysis significant at 1 percent level.

Tree height at seven years of age increased from northern to southern provenances and then declined for southern Illinois and Mississippi-Texas sources because of winter dieback. The diameter of trees from Ohio, Pennsylvania and Indiana was larger in proportion to height than those of other provenances *(Table 2)*. Average DBH differences among provenances were not significant except for the southern provenances and the trees of South Dakota origin.

The Missouri provenance led in numbers of large trees with eight of the ten tallest families and four of the ten largest families in diameter. It appears to be the most promising source of fast growing trees for Nebraska. However, the differences between Missouri and local Nebraska

Table 2. — Total height and DBH, their ratios and bark thickness among cottonwood provenances from different geographic regions.

Provenances	Height Age 7	DBH at Age 7	DBH Height Ratio	Bark Thickness
	m	cm		cm
South Dakota	8.1	8.2	1.04	0.8
Nebraska	10.8	13.9	1.26	0.7
Kansas	11.6	14.3	1.19	0.7
Minnesota-Wisconsin	10.2	12.2	1.17	0.8
N. Illinois	10.6	13.2	1.23	0.9
Missouri	12.1	14.8	1.19	0.7
S. Illinois	9.2	11.0	1.12	1.0
Mississippi-Texas	5.8	4.8	1.00	0.9
Indiana	10.1	13.7	1.32	1.1
Ohio-Pennsylvania	10.5	15.1	1.40	1.2
S. Ohio	10.9	14.5	1.30	1.2
Means	10.15	12.60	1.22	0.9
LSD (0.5)	1.52	2.64	0.11	0.12
LSD (0.1)	1.99	3.44	0.14	0.16

and Kansas porvenances in average total height is not statistically significant *(Table 2).* Growth rate improvement would be enhanced by combined provenance and within provenance selections in view of the large variance components of family and clone *(Table 1).* Ranking in total height among provenances was considerably different between the first two years and the 7th year measurement, but stayed relatively the same after the third growing season. Minnesota-Wisconsin and South Dakota provenances made better than average growth in the early life of the plantation, but lost that advantage in later years to Missouri, Ohio and other provenances *(Figure 3).* The initial growth rate may have been related to early root development of the cuttings (Wilcox and Farmer 1968; Ying 1974).

Correlation between the height at 1973 and that at early ages using family and clone means as items is given in *Table 3.* Correlation coefficients tended to increase as age increased. Other research has had comparable results (Mohn and Randall 1971). About 70 percent of the tallest 10 percent of clones in 1973 were also the tallest in 1969. Hence, early selection for growth rate appears to be possible with relatively small chance for significant error.

Table 3. — Phenotypic correlation coefficients showing the relationship between the height at age 7 (1975) and that at younger ages from 1967 to 1972.

Level of Means	1967	1968	1969	1970	1971	1972
	Year of Measurement					
Family	0.61	0.73	0.85	0.89	0.93	0.96
Clone	0.67	0.76	0.85	0.88	0.90	0.95

Comparisons of growth rate and mortality in this plantation with one from Minnesota of similar sources and purpose suggests strong site effect and seed source-site interactions (Dhir and Mohn 1974). Trees originating from Nebraska and farther north survived equally well in both the Minnesota and Nebraska plantations. Those originating south of Nebraska suffered much higher mortality in Minnesota than in Nebraska. Mean height and diameter of the plantations after six growing seasons was 8.2 m. and 10.4 cm., respectively, in Nebraska and 6.5 m. and 8.6 cm. in Minnesota. While growth of the Minnesota provenance was average in the Nebraska planting *(Table 2),* a similar source was second best in the Minnesota planting. Missouri trees averaged 13 percent taller than trees of Nebraska origin in the Nebraska plantation but they were smaller than the Nebraska trees in the Minnesota planting. Strong north-south interactions were found in several coniferous species provenance tests in the north-central United States (Wright 1973).

Source-site interaction appears to be related to photoperiod, winter temperature and hardiness. Pauley and Perry (1954) found that height growth cessation of *Populus* was a result of an interaction between the individual tree's genotype and photoperiod. The latter functions as a timing device for onset of dormancy. When cottonwood trees of southern origin were planted in more northernly locations, the longer daylength would delay onset of its dormancy as the growing season came to an end. As a result, tissue was too succulent to withstand a sharp drop in temperature. The result was injury, a death of part or all of the crown. Importance of genotypesite interaction in cottonwood has been recognized by Mohn and Randall (1973). Therefore improvement of cottonwood should be aimed at developing strains for well-defined environmental conditions.

Bark and Branch Characteristics A rough thick bark was associated with eastern provenances and smooth thin bark was characteristic of western and northern provenances *(Figure 4, Table 2).* Bark character was extremely variable among and within provenances *(Table 1).* Much of the variation among clones was associated with provenance (31 to 37 percent). Differences in tree size and scoring error rather than site effect inflated the within-clone (among ramets) variation (29 to 38 percent). Bark roughness and thickness were highly correlated (0.82).

A dense crown with numerous small, short branches was characteristic of northern and western provenances while eastern sources tended to have a spreading crown with long large branches *(Figure 5).* Trees of the Missouri provenance were similar to those of Nebraska and Kansas with relatively smooth, thick bark, but 58 percent had an open with a wide distance between branches *(Figure 5,* photo 3). Cottonwood of Northern Iillinois origin had a high fre-

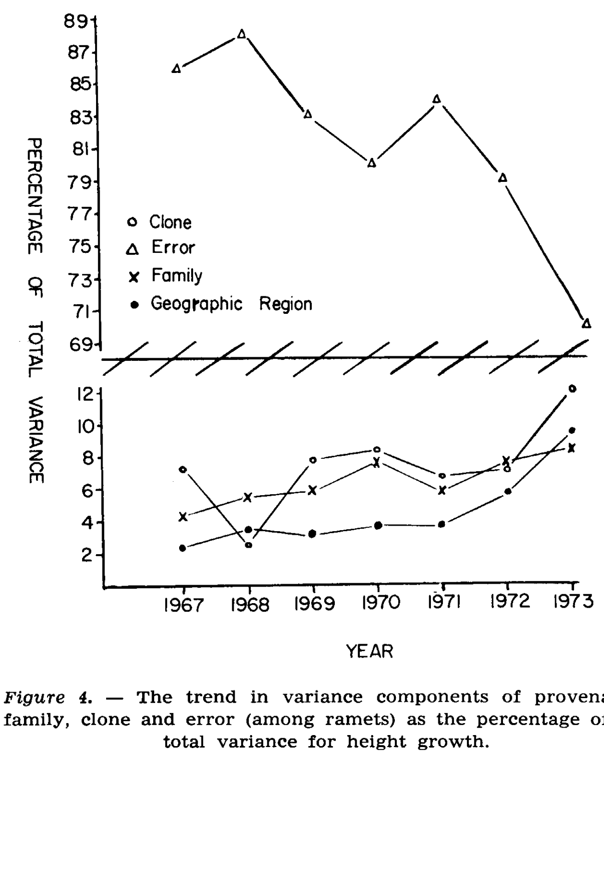

Figure 4. — The trend in variance components of provenance, family, clone and error (among ramets) as the percentage of the total variance for height growth.

quency of intermediate types in both branch and bark characteristics, but trees of Southern Illinois provenances more closely resembled those of Ohio-Indiana. Ohio-Indiana provenances were rated as having the most trees with straight stems and Nebraska and Kansas provenances had the fewest trees of good form. High within-clone variation (70 percent) indicated that stem form of cottonwood was very sensitive to modification by site.

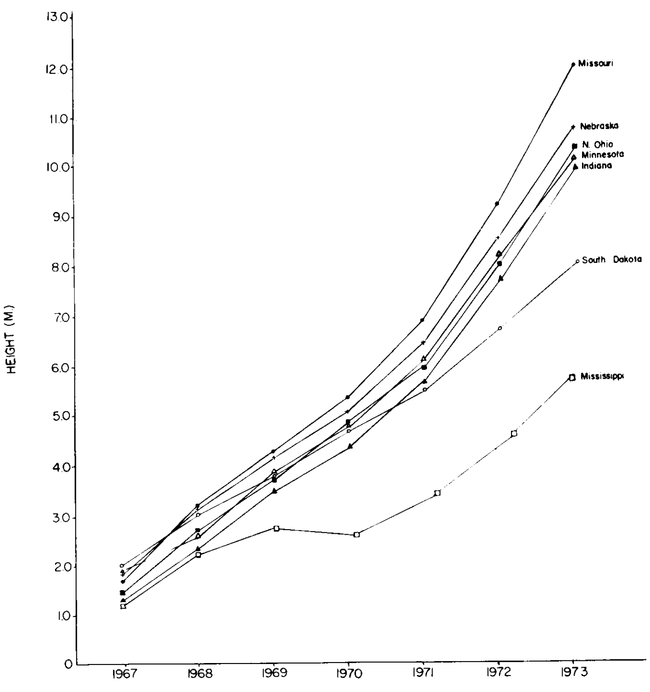

Figure 5. — Comparison of cumulative mean height growth from 1967 to 1973 among seven provenances planted in eastern Nebraska.

Very little is known about inherent patterns of stem form, branching, and bark characteristics. PANETSOS (1969) reported that branching character of *P. deltoides* behaved as a dominant character in combination with *P. nigra* and acted as recessive trait in combination with *P. trichocarpa*. ZUFA (1969) found that stem form of *P. nigra* was inherited as a dominant character and involved more than two genes.

Phenological Observations Variance analyses indicated that date of leaf flushing and anthesis was significantly affected by provenance, family and clone *(Table 4)*. Small error (ramets within clone variability) and interaction variance components suggest that these events are under strong genetic control and their sequences from year to year are predictable. This agrees with other research (FARMER 1966, and 1970). High correlation between observed years (0.89 and 0.84 for flushing and anthesis respectively) further confirms this point.

Variance components of family and clone combined were more than twice that of provenance suggesting wide within provenance variation. A high degree of within-population variation in leaf flushing and flowering has been reported for cottonwood and oher species in native stands and experimental plantations (BARNES 1969; FARMER 1966 and 1970; ROCKWOOD 1968).

The differences in leaf flushing dates among clones within families ranged from 0 to 11 days with an average of 4 days, and anthesis ranged from 0 to 9 days with an average of 3 days. Chis quare tests were made to check the

Table 4. — Estimates of variance components for phenological observations expressed as percent of the total variation.

Source of Variation	DF	Start Anthesis 1973	Start Anthesis 1974	Start Anthesis Comb. 1/	DF	Leaf Flushing 1973	Leaf Flushing 1974	Leaf Flushing Comb. 1/	Leaf Drop (90%)
Provenances	10	11*	15*	8*	10	33*	24*	22*	56*
Families/P	83	43*	32*	21*	100	26*	36*	25*	10*
Clones/F	186	32*	40*	15*	362	33*	29*	24*	18*
Ramets/C	260	14	13	8	773	8	12	10	16

* Variance ratio from variance analysis significant at 1 percent level.

[1]) Variance components for year and year and other factors interactions accounted for 39 and 9 percent for anthesis and 12 and 6 percent for leaf flushing in the combined analysis.

within-family variation for various segregation ratios. There was no discontinuous pattern of variation.

Dates of leaf flushing ranged from April 18 to May 5 in 1973 and April 14 to May 1 in 1974, but most clones flushed during the period April 20—26 in both years. Anthesis ranged from April 7 to 21, but most clones flowered between April 11 and 14 in both years, and completed pollen dispersal in six days. Generally, trees from the north and west of the natural range flushed and flowered first, followed progressively by those from the south and east. However, in view of high within-provenance variation, caution is necessary when interpreting geographic variation. Trees from southern Ohio were significantly earlier than those from the nearby Ohio-Pennsylvania provenance to the east *(Table 5)*. ROCKWOOD (1968) observed no definite latitudinal pattern for leaf flushing in a two-year-old plantation containing origins confined to the Mississippi River. However, a study by ELDRIDGE, *et al.* (1972) indicated a prevalent south-north variation pattern.

Correlation between leaf flushing and anthesis was highly significant over entire provenances (r = 0.7) and also within groups of provenances (r-value ranging from 0.74 to 0.93) indicating their cause-and-effect relationship. Difference in time of flowering among trees, resulting in differential pollination, are of considerable concern in breeding and seed orchard management. Strong correlation between leaf leaf flushing and anthesis provides a method for predicting at the seedling stage when the trees will flower.

Significant correlation between time of anthesis and capsule flower per catkin ratio (r = 0.64) suggests that fewer flowers per catkin were pollinated and developed to maturity on early flowering clones. Frost damage may have caused the reduction of capsule yield.

Seed dispersal ranged from mid-May to late July with Missouri trees generally latest in the Nebraska plantation. However, the difference between the earliest and the latest Missouri clones was two months and considerable variation was found among trees from within other provenances. Variability in time of anthesis and seed dispersal has ecological significance for survival (FARMER 1966).

Variation in leaf drop was mostly associated with provenance *(Table 4)*. Northern origins dropped leaves earliest *(Table 5)*. High correlation with latitude of seed origin (r = 0.82) indicates a strong north-south trends for leaf drop and suggests that photoperiod is the key agent controlling cessation of growth (PAULEY and PERRY 1954).

Progenies of a pioneer species such as cottonwood frequently occupy habitats considerably different from their parents. Under such circumstance, a species must maintain genetic diversity in order to survive (REHFELDT and LESTER

Table 5. — Characteristics of phenology among cottonwood provenances from different geographic regions. Average number of days after April 1 for each provenance.

Provenances	Anthesis		Leaf Flushing		Leaf Drop (90%)
	1973	1974	1973	1974	1973
	days after April 1				DATE
South Dakota	16	14	27	24	183 (Sept. 30)
Nebraska	14	11	24	23	201 (Oct. 18)
Kansas	13	10	23	22	202 (Oct. 19)
Minnesota-Wisconsin	14	11	24	22	191 (Oct. 8)
N. Illinois	14	11	25	23	195 (Oct. 12)
Missouri	13	10	25	24	209 (Oct. 26)
S. Illinois	12	11	25	24	214 (Nov. 1)
Mississippi-Texas	12	11	26	25	221 (Nov. 8)
Indiana	17	16	30	28	207 (Nov. 24)
Ohio-Pennsylvania	15	12	28	26	204 (Nov. 21)
S. Ohio	13	10	23	21	211 (Oct. 28)
Means	13.9	11.0	24.8	23.0	200 (Oct. 17)
LSD (0.5)	2.1	2.7	2.0	2.4	5.0
LSD (0.1)	2.7	3.5	2.6	3.2	6.5

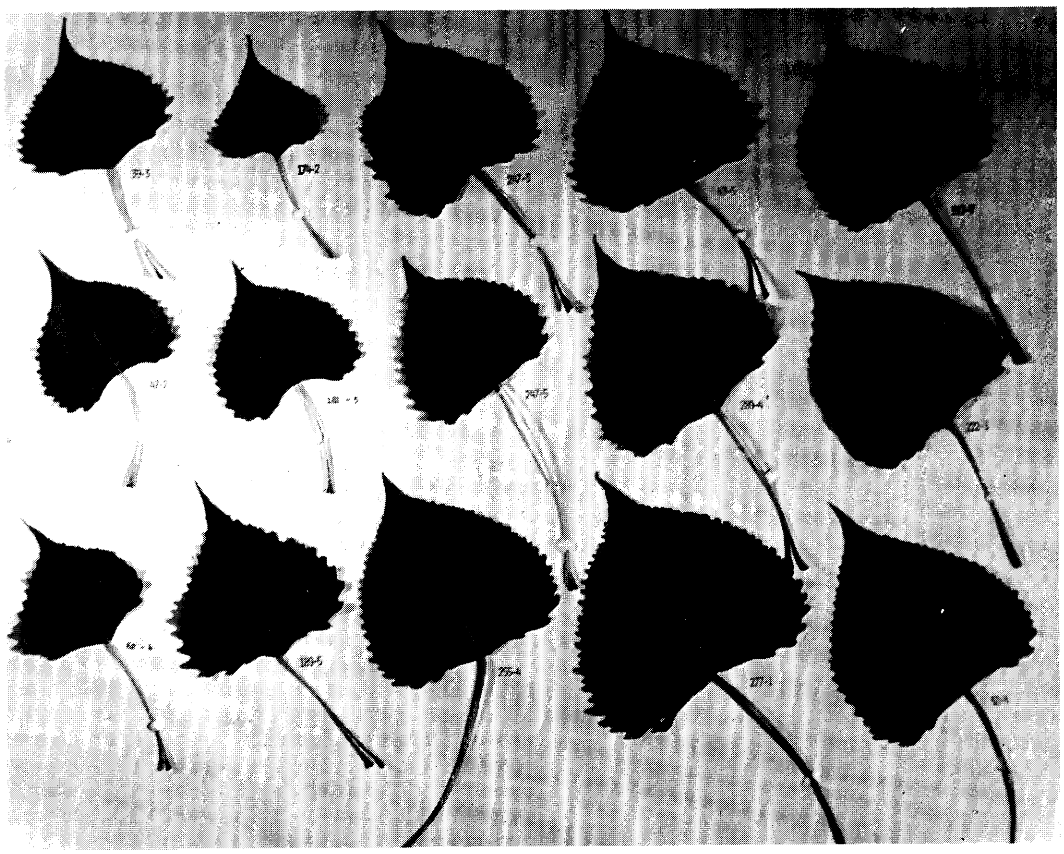

Figure 6. — Leaf size ranged from small on trees from western provenances to large on the eastern trees.

1969). High within-provenance variability reflects a high heterogeneity within the parent population and indicates a high potential for species adaption to varied environments.

Leaf Morphological Characteristics Leaf variability was associated with geographic region and clones within family. The effect of family was not statistically significant *(Table 6)*. Leaf size, gland number, and petiole length, to a lesser degree, exhibited a gradient geographic variation pattern from northwest to southeast *(Figure 6, Table 7)*. These characteristics are useful in delineating different geographic types of cottonwood (MARCET 1961). However, CURTIS and LERSTEN (1974) stated that differences in gland number may change as the growing season progresses.

Some leaf characteristics such as leaf base shape and undulation of leaf surface are extremely useful for clonal identification.

Table 6. — Estimate of variance components for leaf character expressed as percent of total variation.

Source of Variation	DF	Size	Petiole Length	Lamina length Leaf width Ratio	Glands
Provenance	10	58*	26*	16*	58*
Families/P	35	4	7	14*	3
Clones/F	110	25*	36*	36*	20*
Within Ramet	619	13	31	34	19

* Variance ratio from variance analysis significant at 1 percent level.

Table 7. — Leaf character among cottonwood trees from different geographic regions showing gradient variation from north and west to south and east.

Provenance	No. of clones measured	Size	Petiole length	Lamina length leaf width ratio	Glands
		cm²	cm		no.
South Dakota	1	31.1	5.2	1.05	0
Nebraska	20	34.4	7.1	1.06	1
Kansas	6	32.8	6.7	1.05	1
Minnesota-Wisconsin	27	40.5	6.9	1.05	2
N. Illinois	24	53.9	7.2	1.01	2
Missouri	20	51.6	8.6	1.04	3
S. Illinois	7	67.1	8.6	1.09	4
Mississippi-Texas	7	58.5	7.9	1.12	3
Indiana	16	72.7	8.1	1.06	3
Ohio-Pennsylvania	12	69.2	7.9	1.12	3
S. Ohio	15	62.6	8.6	1.10	3
Means or total	156	52.5	7.7	1.06	2
LSD (0.5)		9.60	0.94	0.06	0.73
LSD (0.1)		12.65	1.24	0.08	0.96

Catkin and Capsule Characteristics Variation of catkin and capsule characteristics was mostly associated with individuals within families. Clones of Missouri, Southern Illinois, Indiana and Ohio-Pennsylvania origins had longer pistillate catkins with more flower per catkin. Capsules with longer than average penduncles were more frequent among Missouri clones. Missouri, Ohio-Pennsylvania and Southern Ohio clones had significantly longer staminate flower bud seals than those of Nebraska, Kansas and Minnesota. Catkin and capsule characteristics are very useful in clonal identification because they are less subject to modification by environment.

Most staminate catkins vary from light red to purple prior to anthesis. An exception was anthers of five clones from four Kansas and Missouri families which were predominantely yellow. Sargent (1933) listed yellow anthers as one of the characteristics differentiating *P. sargentii* from *P. deltoides*. This character should not be considered unique to cottonwood of western plains, because it occurs among progenies of families well within the range of eastern cottonwood.

Sex Ratio Sex has been identified on 198 male and 179 female clones. Two clones belonging to one family (138) have both male and female flowers on the same tree with staminate flowers dominating in one clone and pistillate flowers dominating the other. The chi-square test for sex ratio indicated that the number of male and female clones fits the 1 : 1 segregation ratio (Farmer 1964; Jokela 1964). Except for flower traits, we detected no differences between male and female trees which agrees with Jokela's (1964) findings. Hence, there is no reason to favor one sex over another except in situations where the cottony seed presents problems.

Pattern of Geographic Variation Geographic variation in cottonwood appears to be continuous or clinal rather than discontinuous or ecotypic. Most traits investigated exhibited a gradient variation from north and west to south and east. Overlapping was found among progenies for most traits which indicates the occurrence of gene exchange among adjacent populations over the species range. However, a continuous pattern of variation of leaf flushing may be interrupted due to adaptation to local conditions (Nienstaedt 1974).

Analyses of correlation between progeny traits and latitude and longitude of seed sources showed that with the exception of height growth and leaf drop, a majority of the characters investigated had stronger east-west than north-south differentiation. Tle main rivers along which cottonwood is distributed run either north-south (Mississippi), northwest-southeast (Missouri), or northeast-southwest (Ohio). Waterways are probably the main migration route of cottonwood since their seeds stay viable in water much longer than in air (McKnight 1968). Weak north-south differentiation appears to be related to constant migration along the rivers.

European poplar experts recognize three varieties or subspecies within eastern cottonwood from north to south, but with no generally agreed boundary lines (FAO 1958; OEEC 1951). This can be expected in view of the fact that most of the traits studied showed continuous variation.

Summary

Variation of growth, morphological and phenological traits of eastern cottonwood, *Populus deltoides*, followed a clinal pattern from north and west to south and east in a seven year old eastern Nebraska plantation of provenances representing a major part of the natural range of the species. A great potential exists for improvement by selection and breeding because of great heterogeneity of the cottonwood population.

Over 90 percent of the clones from south of 33 degrees N. latitude died or suffered severe winter injury. The tallest trees after seven growing seasons were of Missouri origin. Ohio-Pennsylvania trees led in diameter growth. Ranking in total height among provenances remained about the same after the third growing season. Correlation between height at age 7 and that at younger ages at family and clone level was good (0.61 to 0.96). Early selection is feasible.

Rough thick bark, long large branches, large leaves with large numbers of glands characterized trees of Ohio, Pennsylvania and Indiana. Many clones of Southern Illinois and Mississippi were similar to those of Ohio, Pennsylvania and Indiana. Trees of Minnesota and Wisconsin origin tended to be similar to those of Nebraska, Kansas and South Dakota with smooth bark, small branches and small leaves with few or no glands and few serrations. Leaf flushing and anthesis were highly correlated. The number of male and female clones fits the 1 : 1 sex ratio and no differences were detected between the sexes.

Key words: cottonwood, *Populus deltoides*, provenance test, genetic variation, growth rate, phenology.

Zusammenfassung

Im Jahre 1966 wurde in der Nähe von Mead, Nebraska, USA (40° nördl. Breite), ein Provenienzversuch mit 498 Stecklingsklonen aus 116 frei abgeblühten Familien von

Populus deltoides BARTR. aus dem gesamten Verbreitungsgebiet von Süd Dakota im Norden bis Mississippi und Texas im Süden sowie Ohio und Pennsylvania im Osten angelegt. Die Untersuchung bis zum Alter 7 auf Höhe und Durchmesser sowie auf morphologische und phaenologische Merkmale ergab ein klinales Muster vom Norden und Westen zum Süden und Osten des Verbreitungsgebietes hin. Über 90% der Klone von Herkünften südlich des 33. Breitengrades fielen ganz aus, bzw. litten unter der Winterkälte. Die größten Höhen wurden von Herkünften aus Missouri, die größten Durchmesser von Herkünften aus Ohio und Pennsylvania erreicht.

Literature Cited

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Further Studies on the Ortet-Ramet Relationship in Wood Characteristics of Pinus radiata

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Introduction

An initial investigation of the wood characteristics of ortets and the associated ramets (NICHOLLS and BROWN 1971) revealed important differences between the two groups which were attribued to the effects of topophysis and cyclophysis[4]). On the average the ramets exhibited longer tracheids, larger spiral grain angles and less dense wood than the ortets. This work was followed by a comparison of the wood characteristics of grafted ramets derived from mature ortets and open-pollinated offspring of the same ortets, both of the same age and growing under the same conditions (NICHOLLS *et al.* 1974). The later findings generally supported those of the initial investigation.

The present study is a report of further evidence of the effects of topophysis and cyclophysis based on an examination of material from two lots of *P. radiata* ortets and their associated ramets with the following emphases:

Part 1 — South Australia. Ortets sampled both at breast height and at an upper crown position in the stem and second stage ramets (derived from first stage ramets) sampled in addition to first stage ramets (derived from first stage ramets) sampled in addition to the first stage ramets (derived from ortets).

Part 2 — Australian Capital Territory. Minimal age difference between ramets and ortets. Cuttings were collected when the ortets were 5 years old compared to 35 years for the South Australian ortets in the case of the first-stage ramets.[4])

Part 1. Ortets and Ramets from South Australia

The upper ortet specimens should provide wood char-

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[4]) Cuttings or grafs are said to show topophysis (SEELIGER 1924) when they retain the characters of that part of the shoot (i.e. position on the tree) from which they arise, and cyclophysis (MOLISCH 1915) when they preserve the characters associated with the age of the shoot from which they orginate.