VARIATION IN GROWTH RATE AND TIME OF FLOWERING AND FOLIATION OF EASTERN COTTONWOOD

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Abstract.--Eastern cottonwood (Populus deltoides Bartr.) from central Missouri were tallest, averaging 12.5 m. at age seven in a provenance test near Mead, Nebraska. Ohio trees were larger in diameter than other sources.

Flower and leaf emergence occurred over a two-week period. Leaf flushing and flowering are highly correlated. Generally trees from north and west regions foliated earlier than those of eastern origin, but variability was found among progenies from Missouri and Illinois: Leaf drop date was strongly correlated with latitude of seed origin and occurred from early September to late November.

Additional keywords: Populus deltoides, cottonwood provenance test, family, clone, phenology, height growth, diameter growth.

Growth rate is usually the most important selection criteria in most breeding programs. Improved growth rate of cottonwood (Populus deltoides) through selection has been well documented. Johnson (1972) reported several clones exceeded the controls by 13 percent in diameter growth and 10 percent in height growth after five years of growth. Variation in phenological characteristics are also important in tree breeding. Information about cottonwood phenology, however, has been obtained mostly from seedlings and confined to local populations (Farmer 1970, Rockwood 1968, Wilcox and Farmer 1967). This paper reports growth and phenological variation in a regional cottonwood provenance test over seven growing seasons from 1972 to 1974.

METHODS

In 1966, a provenance plantation of 498 clones of cottonwood (Populus deltoides Bartr.) belonging to 116 open-pollinated families was established near Mead, Nebraska, by planting unrooted cuttings. The collection of plant materials was obtained from the Department of Forestry, University of Illinois, through cooperative regional tree improvement project NC-99. An additional clone from South Dakota of unknown location was also included. Clones within the planting were completely randomized with three replications of single tree plots. Eleven geographic regions were delineated to facilitate comparisons (fig. 1).

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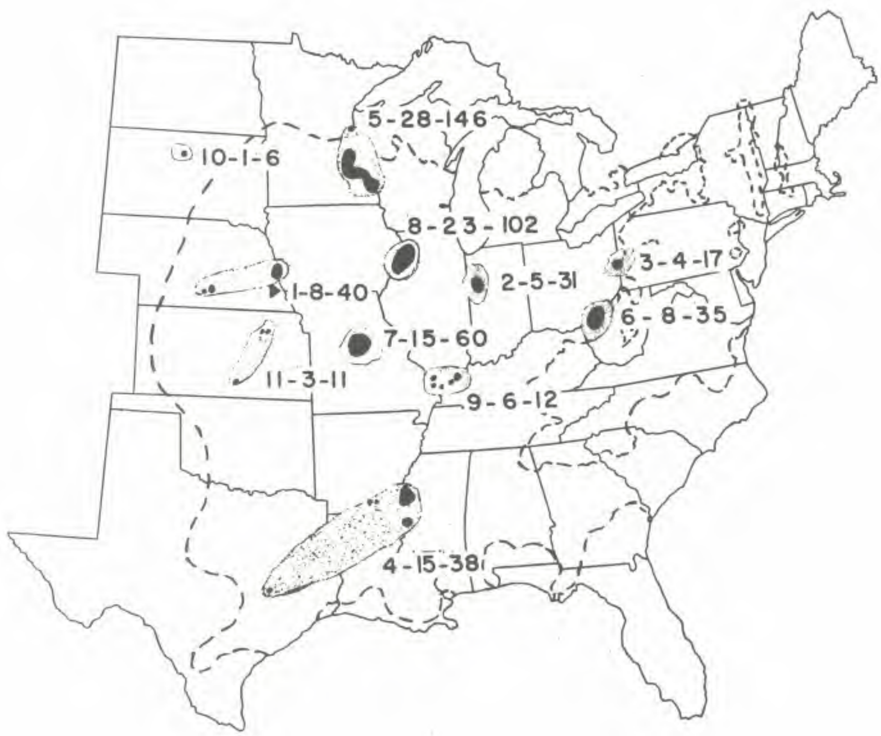

Figure 1.--Natural range of eastern cottonwood (bounded by dashed lines), location of the seed trees (black), and geographic regions delineated for statistical analysis (shaded). Numbers designate geographic region and number of seed trees and clones within each region, respectively. The triangle denotes the location of the plantation.

Annual height measurements from 1967 and diameter (DBH) measurements from 1970 through 1973 were recorded. Dates of leaf flush, anthesis, and leaf fall were recorded for the years 1972-1974.

The following procedures were used in making phenological observations:

1. Leaf flush: leaf bud opening in the upper half of the crown was noted by recording the number of days after April 1 required for leaf shape to become recognizable.

2. Beginning of anthesis: the number of days after April 1 required for shedding pollen. At this stage, male catkins reached full length, became pendulous and the anthers turned yellow. Female flower buds were elongated to 1 to 2 cm. beyond bud scales and stigmas were exposed and very succulent.

3. End of anthesis: the number of days after April 1 required for male catkins to turn black.

4. Period of anthesis: the difference in days between 2 and 3 above.

5. Seed dispersal: the number of days after April 1 required for the opening of the first capsule.

6. Leaf drop: the number of days from April 1 when 50 percent and 90 percent of the leaves dropped, respectively. Only the first stage was recorded in 1972 because of frost.

Variance analysis, F-tests and other statistical techniques assisted in determining the significance of the effects of geographical region, family and clone.

RESULTS

Geographic region, family, and clone affect total height and diameter growth (Table 1). Generally, trees from latitudes south of Nebraska, except those from Mississippi and southern Illinois, grew taller than those from Nebraska and farther north. Trees from Ohio (Regions 3 and 6) generally had a rough, thick bark and were larger in diameter than trees from other regions. Average diameter (DBH) inside bark of Nebraska and Missouri clones was 15.2 cm. as compared to 15.7 and 14.7 cm. diameter inside bark for trees from Regions 3 and 6, respectively. Total height among clones ranged from 5.3 to 16.4 meters and diameter ranged from 3.8 to 23.0 centimeters. Growth rate of Mississippi and southern Illinois trees was apparently impaired by cold injury during the winter (Ying 1974).

Table 1.--Mean height and diameter of trees originating from eleven geographic regions with percentage of clones from each region in the top 72 for height and diameter

Region	Height (Meters) 1967	1973	% clones ranked in Top 72	Diameter (DBH) (Centimeters) 1973	% clones ranked in Top 72
Mo. (7)	1.7	12.5	42	15.2	36
Kans. (11)	2.0	12.2	9	15.4	9
Neb. (1)	1.9	12.0	22	15.9	28
S. Ohio (6)	1.9	11.9	18	16.3	18
S. Ill. (9)	1.4	11.5	30	14.7	20
Ill. (8)	1.9	11.2	11	14.2	11
Ohio (3)	1.6	11.0	25	16.0	38
Ind. (2)	1.4	10.8	7	14.8	20
Minn. (5)	1.9	10.6	10	13.0	7
Miss. (4)	1.1	9.6	0	11.3	0
S. Dak. (10)	2.2	9.5	0	10.8	0
Mean	1.8	11.2		14.3	
S.D.	0.8	2.0		4.0	

The relationship of origin to the 72 largest clones (top 16 percent) is shown in Table 1. Fifty-two of these 72 clones were superior in both height and diameter. The tallest trees came from 45 seed trees and thus represent 45 families. Six families (Nos. 52, 222, 238, 246, 251 and 292) contributed more than 3 of the tallest clones. Three of these families were from Missouri; and two of these (Nos. 238 and 251) contributed 5 clones each. The 72 clones with the largest diameter were distributed among 44 families. Six of these (Nos. 51, 52, 238, 246, 251 and 277) contributed more than three clones each. Three of these were from Missouri; and again families 238 and 251 contributed the largest number of progenies in the top 16 percent (4 clones each).

The tallest 72 clones had a mean total height of 13.5 m. as compared to the plantation mean of 11.2 m. The 72 clones with the largest diameter had a mean DBH of 19.0 cm. as compared to a mean of 14.3 cm. for the entire plantation.

Correlations based on clone means between the height at age 7 and that at younger ages from 1 to 6 ranged from 0.67 to 0.95. Correlation between height and diameter at the same age was high (0.83 to 0.93).

Variance analysis indicated that date of leaf flushing, flowering, seed dispersal, and leaf drop was significantly affected by geographic region, family, clone, and year of observation. Years by other factor interactions were statistically significant in most cases, but the variance components for interaction terms were much smaller than those of main factors. For example, in date of leaf flushing, variance components for all interaction terms account for only 6 percent of the total variance as compared to 83 percent for the main factors.

Actual dates of leaf flushing ranged from April 14 to May 1 in 1974 and April 18 to May 6 in 1973. Most clones flushed between April 20 and 26 in both years. Range of flushing dates varied among the clones from different regions. About 90 percent of progenies from the north and west part of the sampled areas (Nebraska, Minnesota and Kansas) completed leaf flushing before April 25; whereas, 90 percent of those from the east (Ohio and Indiana) flushed after April 25. It appears that clones from Missouri and Illinois are intermediate types, with over 80 percent of the flushing between April 21 and April 27, with about equal numbers of very early and very late types. Trees from Region 6 did not follow this variation pattern. The variation within regions was greater than among regions in most cases. The differences in leaf flushing among clones within families ranged from 0 to 11 days (fig. 2).

Anthesis (initial dehiscence of anthers and initial receptivity of stigmas) averaged about 10 days ahead of leaf flushing but showed a similar variation pattern. Progenies from Regions 2, 3 and 10 flowered later than others (Table 2) with the beginning of anthesis ranging from April 7 to 21. Most clones flowered between April 11 and 14 in both years and completed pollen shedding in six days.

Table 2.--Mean days after base date of April 1 for appearance of phenological phenomena arranged from early to late for leaf flushing

Region	Flush	Beginning of Anthesis	End of Anthesis	Seed Dispersal	Leaf Drop (90%)
			Number of Days		
Kan. (11)	22	12	18	61	202
S. Ohio (6)	22	11	18	69	211
Minn. (5)	23	12	17	62	191
Neb. (1)	23	12	18	71	201
Miss. (4)	24	--	--	--	221
Ill. (8)	24	12	18	64	195
S. Ill. (9)	24	11	16	75	214
Mo. (7)	25	12	18	89	209
S. Dak. (10)	25	14	17	62	173
Ohio (3)	27	13	19	60	204
Ind. (2)	29	17	22	61	207
Plantation Mean	24	12	18	71	200
S.D.	1.2	1.1	1.0	6.0	4.8

1/ Mean for leaf flushing and flowering characteristics are the average of 1973 and 1974. Leaf drop and seed dispersal are based on the average of one year, 1973.

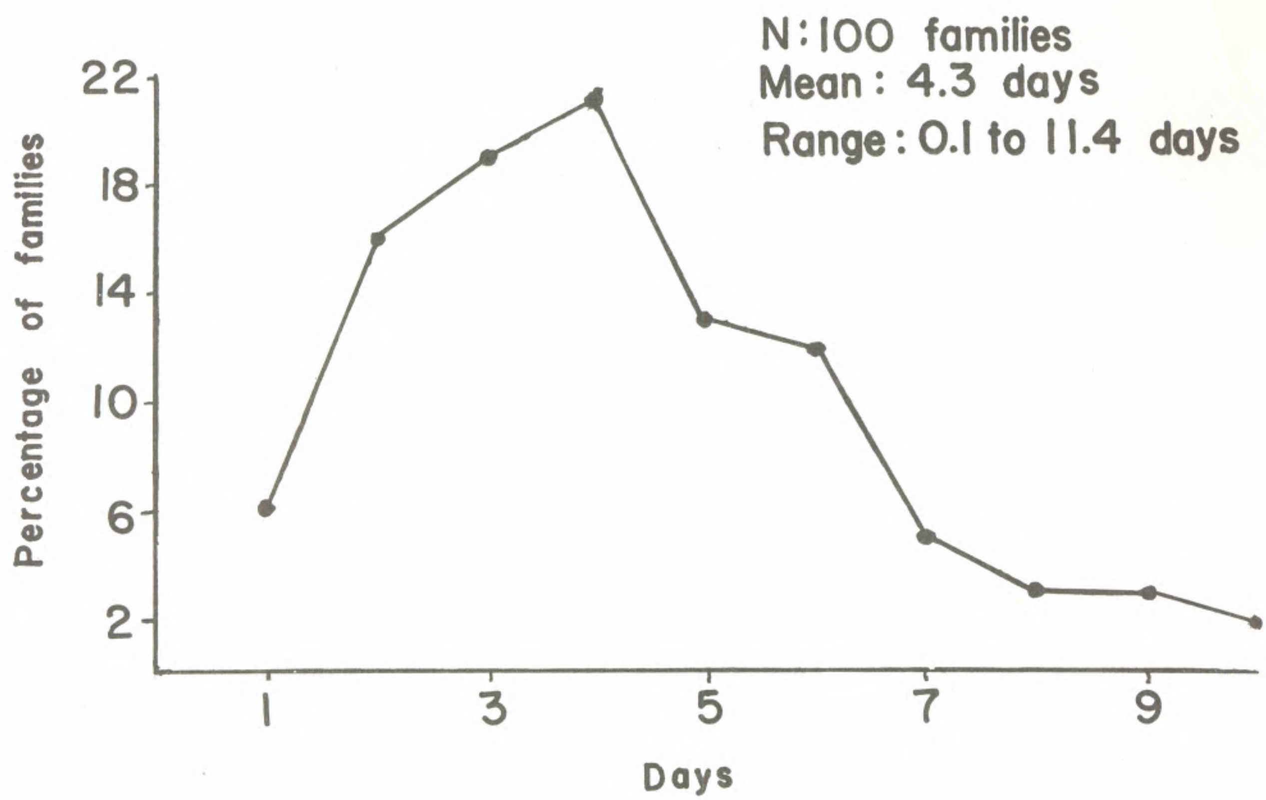

Figure 2.--Frequency distribution of the mean differences of leaf flushing date between the earliest and the latest clones within each family.

The differences in leaf drop were mostly associated with geographic regions. Most trees from South Dakota and Minnesota dropped over 90 percent of their leaves in late August or early September, but those from Mississippi and Arkansas did not reach that stage until mid- or late-November. Correlation between the stages of 50 percent and 90 percent leaf drop was very high ($r = 0.94$).

Seed dispersal ranged from late May to late July with Missouri trees generally the latest. However, the difference between the earliest and the latest clones from Missouri was about 2 months, and considerable variation was found within other regions.

Of all the phenological characteristics studied, only leaf drop date was strongly correlated with latitude of seed origin ($r = 0.86$). Correlation coefficients between leaf flushing and latitude are less than 0.20.

Leaf flushing and anthesis date was highly correlated (fig. 3). The regression coefficient (b-value) was significant at the 0.01 level of probability. Variation due to regression accounts for 53 percent of the total variation ($R^2 = 0.53$). We found no correlation between phenological characteristics and growth rate. Correlation coefficients between the two observed years for leaf flushing is 0.86 and 0.77 for anthesis.

A total of 377 clones (198 male and 179 female) have been sex-identified. Two clones belonging to the same family, 138-4 and 138-6, have both male and female flowers on the same tree. Staminate flowers dominate in clone 138-6, ovulate flowers dominate in 138-4. Differences between sexes for traits were not statistically significant, indicating no correlation between sex, growth, and phenological characteristics. The Chi-square test for sex ratio indicates it fits the 1:1 segregation ratio.

DISCUSSION AND CONCLUSIONS

Trees from some sources, especially those from South Dakota and Minnesota, made better than average growth during the first two growing seasons (1967 and 1968), but did not retain that advantage in succeeding years. The reason is probably that since unrooted cuttings were used to establish the field planting, the initial growth rate may have been related to ability to establish a strong root system immediately after planting. Significant and positive correlation between root number in a certain period of time in the rooting test and the first year height of the clones on the plantation was found (Ying 1974). After the rooted cuttings became established, other hereditary characteristics governing rate of growth became dominant factors. Thus, some of those cuttings which started slowly became the largest trees in the plantation seven years after planting.

A high combining ability of parent trees is indicated in Families 238 and 251 from Missouri with 5 out of 6 progenies ranked in the top 16 percent for size.

Selection of a group of clones with desirable characters for immediate commercial use or creating a base population for the breeding of advanced generations would logically be the next step in any breeding program. Wide

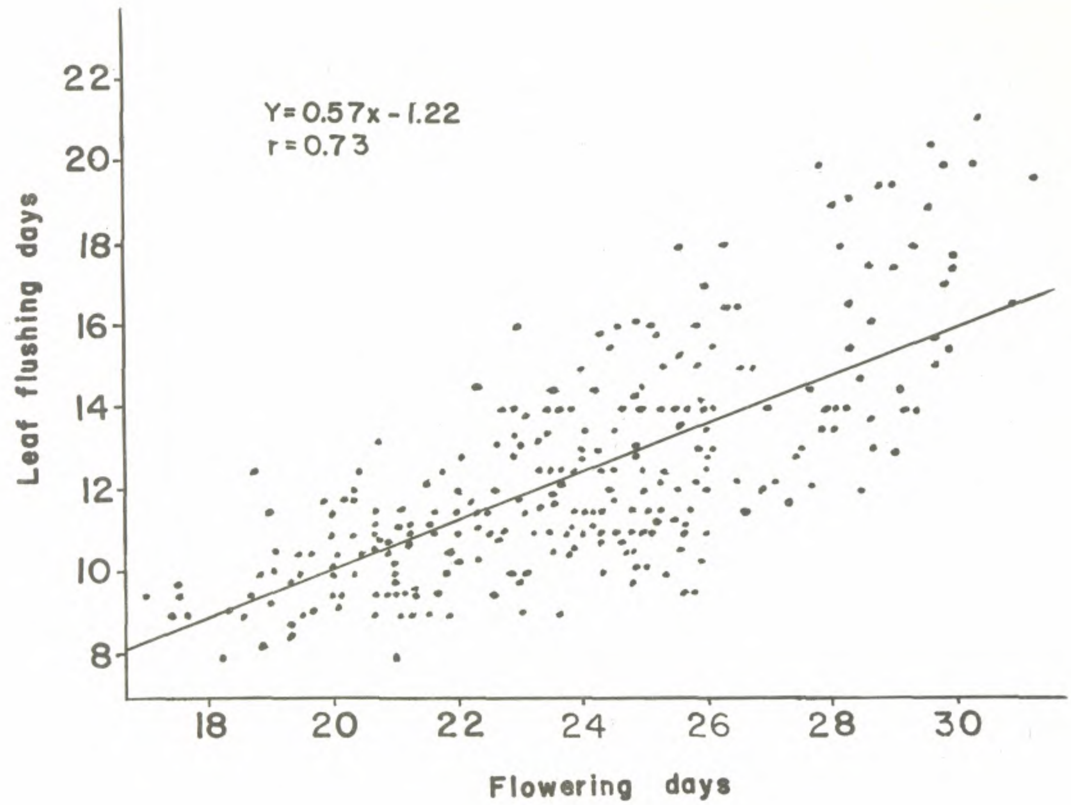

Figure 3.--Relation between leaf flushing and anthesis based on mean days after April 1 for 1973 and 1974.

variation in growth rate among clones suggests the possibility of improvement through selection. However, if we select the top 72 clones for breeding materials or a seed orchard, most of them will be from a few geographic regions and the relationship among many of them will be half-sib. An important consideration will be the possible effect of inbreeding. We have no knowledge of inbreeding effect upon cottonwood, but deleterious effects from selfing of pine species have led tree breeders to believe that maintaining genetic diversity is very essential in a long range tree breeding program.

The stage when flowers extended 1 to 2 cm. from the bud scale was arbitrarily chosen as the date of anthesis for the female trees because stigmas were probably receptive at this time. At this time the stigma was exposed and very succulent. Three or four days later the flower length had more than doubled and the stigma surface became dry. The receptive stage was probably at an end. Further research may be required to establish the peak of receptivity in order to facilitate controlled pollination.

Significant differences among geographic regions in date of leaf flushing was reported by Rockwood (1968); but he found no latitudinal or longitudinal variation pattern. McMillan (1957) reported that leafing and flowering advanced progressively from northwest to southeast when he observed these phenological phenomena in native stands in Nebraska. Both McMillan (1957) and Pauley and Perry (1954) showed that temperature rather than photoperiod plays the most significant role in opening of buds. Significant differences in date of leaf flushing and flowering between years and failure of correlation of these phenomena with latitude suggest that environmental factors other than daylength may be more critical in determining breaking of dormancy.

Wide variations in leaf flushing among progenies from the same geographic regions have been observed by Farmer (1970), Wilcox and Farmer (1967), and Rockwood (1968) in experimental plantations. Similar variation was found in the present study. McMillan (1957) observed that adjacent trees in all the populations of eastern cottonwood displayed as great a variation in time of leaf flushing and flowering as that found among populations across the state. Farmer (1966) also reported that differences between trees within stands account for 98 percent of the significant variation in date of flowering time. In our study, small error variance, year by clone interaction components, high correlation between years, and significant differences among members of the same family observed, all indicate that time of bud breaking is genetically conditioned.

Time of leaf flushing is an important factor to be considered in trying to avoid spring frost injury. Wide within-region variability indicates the potential ability of populations to adapt to the variable nature of climatic conditions from year to year. In view of the marked differences in flowering time between clones from some areas found in this study and the differences between proximally located trees in native stands observed by McMillan (1957) and Farmer (1966), such a variation may be an important mechanism for reducing the chance of mating among related individuals. From a practical breeding standpoint, this variation must be taken into consideration when we make a selection of a group of clones for a seed orchard and hope that random mating and a free exchange of genes among them will occur. High correlation between leaf flushing and flowering makes it possible to predict flowering patterns from leaf flushing at seedling stage. It was further noted that the very early flowering clones did not produce as much seed although they appeared to have as many flowers as the late flowering clones.

Figure 3 shows that distribution of within-family variation is continuous and, therefore, multiple gene segregation can be assumed.

High negative correlation of leaf drop with latitude may indicate the tendency for trees of high latitude (long daylength) origin to enter dormancy late. The conclusion by Pauley and Perry (1954) that the effect of photoperiod (related to latitude) is primarily related to the time of the onset of dormancy, but not to break of dormancy, appears to be confirmed by the results of this study also.

Seed dispersal among clones not only varied in time but also in pattern. Some clones completed seed dispersal in a few days while others required two weeks for dispersal. According to Farmer's (1966) observations in the lower Mississippi Valley, seed dispersal has ecological significance for survival.

Upon the completion of the analysis of other data compiled from the provenance plantation, it should be possible to select a group of clones which have a potential for superior performance within a reasonable distance of Mead, Nebraska. Clones can also be selected which have potential in ornamental or landscape plantings. The plantation also will provide the basis for a breeding program.

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