Variation in Time of Flowering and Seed Dispersal of Eastern Cottonwood In the Lower Mississippi Valley

BY
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Abstract. Flowering of *Populus deltoides* Bartr. occurred from early March to early April; differences between trees within stands accounted for 98 percent of the significant variation in dates. High correlation (r = .91 to .96) between 1963 and 1964 dates of individual trees indicated that trees within stands flower in a predictable sequence. Seed dispersal lasted from mid-May until late August, and most of the variation was accounted for by differences among trees. Moderate correlations (r = .49 to .84) were observed between 1963 and 1964 dispersal dates of individual trees.

IN THE LOWER Mississippi Valley, eastern cottonwood (*Populus deltoides* Bartr.) flowers mostly in March, and seed is dispersed from late spring until late summer. Tree-to-tree variation is considerable, however, and the study described here was designed to delineate patterns of variation preliminary to a genetic investigation of them.

Methods

In 1962, ten 30-foot-wide transects were established in natural 20- to 30-year-old stands on the Mississippi River between Clarksdale and Vicksburg, Mississippi. Transects 1 through 4 were near Vicksburg on sites characterized by heavy clay soils and subject to annual spring flooding. Transects 5 through 8 were on similar sites approximately 150 miles north of Vicksburg. Transects 9 and 10 were on sandy-loam river-front sites 130 miles north of Vicksburg.

The first 60 trees on each transect were selected for observation. In 1963, flowering dates were recorded for all trees which flowered. Transects were visited twice weekly for this purpose, and initial appearance of flowers was observed with binoculars. Trees were further observed at weekly intervals throughout the seed dispersal period; dates of initial, beginning maximum, and final dispersal were recorded for each female tree. Release of seed by one or more catkins was considered initial dispersal. The maximum period was considered started when at least 30 percent of a tree's catkins were dispersing. These observations were repeated in 1964 on five of the ten transects (2, 3, 4, 9, and 10).

Results

Flowering began in early March and continued until early April in both 1963 and 1964 (Fig. 1). Male trees began slightly earlier than female. Individual males dispersed pollen from 3 to 7 days, depending upon the weather. In trees of both sexes, foliation followed flowering

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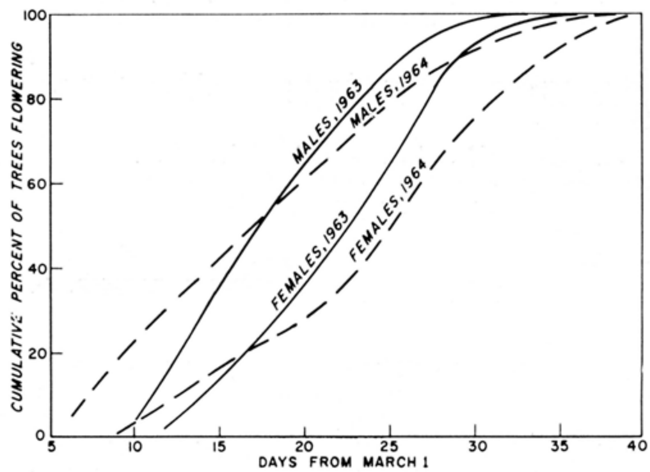

FIGURE 1. *Progression of flowering.*

by 4 to 10 days.

Variation in flowering dates of 50 trees on each of transects 2, 3, 9, and 10 in 1963 and 1964 was analyzed using the model outlined in Table 1; the unit of analysis was the number of days from March 1 until initial flowering. Differences between mean flowering dates at the two locations and between transects within locations were not significant. Differences between trees within transects and between years were significant at the .01 and .05 levels of probability, respectively. Variance components were 1.3 for years and 49.5 for trees within transects. Hence, 98 percent of the observed variation was among individual trees. Figure 2 illustrates variation in flowering and subsequent foliation in a typical stand.

Correlations between the 1963 and 1964 flowering dates of individual trees within transects 2, 3, 4, 9, and 10 were significant and high: r = .91 to .96. Trees

TABLE 1. Analysis of variance—flowering dates in a lower Mississippi Valley cottonwood population.

Source of variation	*df*	Mean square	Estimated mean square
Location (L)	1	80	$\sigma^2_E + y\sigma^2_{R(T)(L)} + yr\sigma^2_{T(L)} + yrt\Sigma\alpha^2/l - 1$
Transect/Location (T)	2	9	$\sigma^2_E + y\sigma^2_{R(T)(L)} + yr\sigma^2_{T(L)}$
Trees/Transect/Location (R)	196	106**	$\sigma^2_E + y\sigma^2_{R(T)(L)}$
Years (Y)	1	271*	$\sigma^2_E + y/y - 1[r\sigma^2_{Y\,T(L)}] + rtl\Sigma\beta^2/(y-1)$
Years × Location	1	8	$\sigma^2_E + y/y - 1[r\sigma^2_{Y\,T(L)}] + rt\,\Sigma\alpha\beta^2/(y-1)(l-1)$
Years × Transect/Locations	2	12	$\sigma^2_E + y/y - 1[r\sigma^2_{Y\,T(L)}]$
Years × Trees/Transects/Locations	196	7	σ^2_E
Total	399		

** Significant at the .01 level of probability; *significant at the .05 level of probability.
$\sigma^2_E = y/y - 1[\sigma^2_{YR(T)(L)}]$

FIGURE 2. *Variation in flowering and foliation within a stand of cottonwood in the lower Mississippi Valley.*

thus flowered in the same general sequence in both years.

Seed dispersal took place between mid-May and late August in both 1963 and 1964. Johnson (1965) reports a similar period. The progression in 1963 is illustrated in Figure 3; dispersal in 1964 followed the same pattern. Estimation of maximum dispersal date was somewhat subjective, but the vertical distance between curves 2 and 3 in Figure 3 is believed to be a reasonable estimate of

TABLE 2. Estimated variance components for seed dispersal events in a lower Mississippi Valley cottonwood population.

Source of variation	Initial dispersal date	Peak dispersal date	Last dispersal date	Total dispersal time
Location	16.0	50.3	161.2	74.6
Transects/Locations	9.7*	28.2**	158.2**	82.9**
Trees/Transects/Locations	29.5**	98.5**	389.5**	281.0**
Years	Negative	2.3	7.0	7.3
Years × Locations	13.5*	46.0*	16.0	Negative
Years × Transects/Locations	Negative	Negative	Negative	Negative

** Source of variation significant at the .01 level of probability; *source of variation significant at the .05 level of probability.

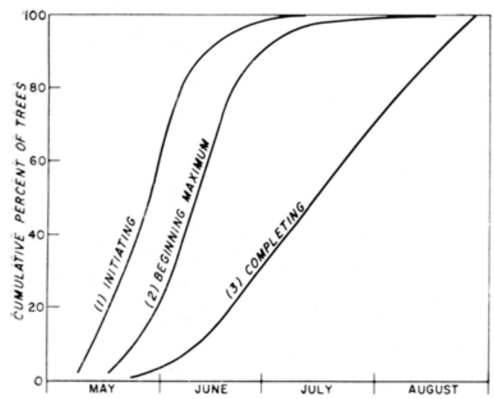

FIGURE 3. *Progression of seed dispersal.*

the percentage of trees dispersing seed on a given date. Thus, maximum was between mid-June and late July. Trees continuing to disperse in late August usually did so on a small scale. Consequently, there was markedly less "cotton in the air" during late summer, although 10 to 20 percent of the trees were still dispersing seed.

Variation in dates of dispersal events among trees on transects 2, 3, 9, and 10 was analyzed with the model outlined in Table 1. Data from the first 20 female trees on each transect were used, and the unit of analysis was the number of days from May 1 to the event. Total dispersal time, the number of days between initial and last dispersal dates of individual trees, ranged from 14 to 91 days. Most of the significant variation was accounted for by differences among trees within transects (Table 2). Transects within locations contributed a smaller, but significant, portion of the variance. Effects of location and year were not significant, but an interaction of year and location contributed significantly to variation in dates of initial and peak dispersal. This interaction is accounted for by relatively early dispersal in 1964 at the location containing transects 9 and 10.

The dates of some dispersal events on individual trees in 1963 and 1964 were significantly correlated (Table 3). Although weaker than correlations between 1963 and 1964 flowering dates, the relationships indicate that dispersal within a group of trees follows the same pattern from year to year. The sequence was especially strict with respect to ending dates (r = .77 to .84). No relationship was observed between tree size and dispersal dates.

Discussion and Conclusions

The wide variation in phenology observed within single stands in this study has been previously reported for *Populus* in other regions by Cottam (1954), Barnes (1959), and McMillan (1957).

TABLE 3. Coefficients of correlation between 1963 and 1964 seed dispersal events in a lower Mississippi Valley cottonwood population.

Event	Transect 2	Transect 3	Transect 4	Transect 9	Transect 10	Mean
Initial dispersal date	0.36	0.49*	0.55**	0.27	0.62**	0.46
Beginning date of maximum dispersal period	.78**	.36	.74**	.62**	.76**	.65
Last dispersal date	.77**	.80**	.78**	.78**	.84**	.79
Total dispersal time	.74**	.71**	.63**	.70**	.79**	.71

** Significant at the .01 level of probability; *significant at the .05 level of probability.

The predictable flowering and seeding sequences indicate that either microclimates within stands are highly variable and predictable from year to year, or that phenology is under strong genetic control. The former hypothesis is considered unlikely on the bottom-land sites studied, especially since no clinal pattern of variation was observed on individual transects. Furthermore, considerable evidence points to strong genetic control of within-population phenological variation in *Populus* and other species (Joachim 1957, McMillan and Pagel 1958, Morris *et al.* 1957). The combination of relatively wide intra-stand variation and predictable tree-to-tree sequences thus suggests strong genetic control of flowering dates and moderate control over seed dispersal events.

The observed patterns of seed dispersal have considerable ecological significance in the lower Mississippi Valley. Cottonwood requires moist, bare mineral soil for germination and establishment. The long dispersal period insures the presence of viable seed on such sites whenever they occur along receding water courses during early and mid-summer.

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