Quantification of Disease Progress and Defoliation in the Poplar Leaf Rust-Eastern Cottonwood Pathosystem

Richard C. Hamelin, Louis Shain, Richard S. Ferriss, and Bart A. Thielges

First and last authors: Department of Forestry, University of Kentucky, Lexington 40546-0073. Second and third authors: Department of Plant Pathology, University of Kentucky, Lexington 40546-0091.

Present address of first author: Laurentian Forestry Centre, 1055 rue du P.E.P.S., Ste-Foy, Qc, Canada G1V 4C7. Present address of last author: College of Forestry, Oregon State University, Corvallis 97331-5704.

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ABSTRACT

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During three seasons, poplar leaf rust epidemics caused by *Melampsora medusae* f. sp. *deltoidae* were compared among families of eastern cottonwood, *Populus deltoides*, derived from natural stands along the Mississippi River valley from Cairo, IL, to Rosedale, MS, and grown in Carlisle County, KY. In 1988 and 1989, families of southern origin were more resistant than their northern counterparts at the test site with regard to the relative area under the disease progress curve (*RAUDPC*), the final disease severity (*Yf*), the rate parameter from the Richards model (*Ra*), and the number of days before defoliation (*DLF*). Cluster analyses using all variables grouped families into northern clusters of susceptible families and southern clusters of resistant families. Significant correlation coefficients were calculated between disease progress variables (*RAUDPC*, *Yf*, and *Ra*) and defoliation variables (*DLF*). Because between 95 and 99% of the variation in *RAUDPC* was explained by one disease observation during the last week of September disease resistance was estimated, in 1990, in 40 families of eastern cottonwood by measuring disease severity and defoliation once in early October. A north-south gradient again was apparent, with families from the north showing more susceptibility than families from the south.

Additional keywords: pathogenic variability.

Poplar leaf rust, caused by *Melampsora medusae* Thuëm. *deltoidae*, is one of the most serious diseases of eastern cottonwood, *Populus deltoides* J. Bartram ex Marsh, in intensively managed plantations (15, 19). Yield losses of 65%, in volume, were reported for hybrid poplars with *P. deltoides* parentage (23).

Species and cultivars of poplar have been reported as varying in their resistance to poplar leaf rust, and breeding strategies have been proposed (19). Heritabilities of poplar leaf rust resistance have ranged between 0.42 and 0.97 in eastern cottonwood families derived from natural stands in Pensylvania, Ohio, Illinois, Missouri, Indiana, and Mississippi (5,20,24).

There is little information concerning the epidemiological parameters of rust resistance in eastern cottonwood. Most epidemiological studies in this pathosystem have been based on discontinous, descriptive rating systems that do not allow quantitative analyses of disease progress curves. In addition, a number of studies use different rust rating scales (e.g., 0–3 [8], 1–7 [20], 0–4 [2], 1–5 [1]), making comparisons among studies difficult.

Taris (18) measured disease severity of poplar leaf rust over time on different cultivars of *Populus* spp. in France, but he may have underestimated disease progress at the end of the season, when defoliation occurs, by failing to adjust disease severities for fallen, diseased tissue. Defoliation has received little attention despite the fact that it represents one of the most important components of this pathosystem. Also, relationships between disease severity and defoliation have not been reported because disease severity and defoliation have often been incorporated into the same rust rating system.

The objectives of this study were to: 1) quantify disease progress and defoliation in genotypes of eastern cottonwood varying in their levels of resistance to poplar leaf rust, 2) study relationships between disease progress and defoliation, and 3) document geographic trends with regard to poplar leaf rust resistance in families of eastern cottonwood derived from natural stands along the Mississippi River valley.

MATERIALS and METHODS

Stand establishment. During the fall of 1985, 10–20 potential parent trees were selected at each of 10 locations along the Mississippi River valley from Cairo, IL (location 1; lat. 37°03′ N), to Rosedale, MS (location 10; lat. 33°45′ N) (Table 1), a distance of 386 river miles (approximately 200 air miles), as part of an eastern cottonwood breeding program (Fig. 1). Selections were based mainly on rust-resistant phenotypes. Secondary criteria included tree form, height, and diameter (21).

Seeds were collected during the spring of 1986, sown in pots containing a peat/perlite mixture, and were grown in a greenhouse until the fall, when they were transplanted in a nursery. In the spring of 1988, 40 surviving half-sib families (siblings sharing one parent) were transplanted on Island-3 of the Mississippi River in Carlisle County, KY (lat. 36°50′ N, long. 89°10′), in a randomized complete-block design containing eight blocks. In each block, the half-sib families were planted in four-tree plots, each plot consisting of four siblings planted at 4-m intervals. For logistical reasons, only the first three blocks were considered in this study. Because of the high levels of endemic inoculum present, no artificial inoculum was introduced.

Disease progress. Disease progress was quantified by recording disease severities periodically, at 7- to 15-day intervals (depending on the accessibility of Island-3), starting in August. Five leaves (leaf positions 5–10) (7,17) were tagged on each of two branches on families from locations 1, 5, and 7–10 and 1, 2, 5, and 7–10 in 1988 and 1989, respectively. Measurements were taken on two and six trees per family in 1988 and 1989, respectively.

TABLE 1. Disease progress and defoliation variables for epidemics of poplar leaf rust on eastern cottonwood derived from natural stands along the Mississippi River valley and grown in Carlisle County, KY

	Location of origin	Number of families	Disease progress and defoliation variables[a]					
			RAUDPC	*Yf*	*Ra* ($\times 10^{-3}$)	*m*	*DLF* (days)	*RHAD* ($\times 10^2$ cm^2 $\times$ day)
1988	1	1	0.124 (0.040)[b]	0.353 (0.121)	13.9 (8.3)	1.54 (0.42)	21.94 (13.06)	3.29 (3.16)
	5	2	0.179 (0.069)	0.428 (0.157)	11.4 (2.5)	1.37 (0.24)	25.97 (8.62)	4.65 (2.60)
	7	1	0.107 (0.042)	0.312 (0.034)	10.5 (4.8)	1.07 (0.07)	36.46 (3.21)	3.43 (0.09)
	8	1	0.025 (0.013)	0.042 (0.016)	2.2 (1.6)	1.63 (0.04)	42.00 (0.00)	9.34 (0.85)
	9	1	0.098 (0.054)	0.148 (0.072)	7.4 (0.3)	1.01 (0.01)	19.94 (9.06)	3.15 (3.05)
	10	3	0.034 (0.012)	0.078 (0.039)	4.7 (3.1)	1.25 (0.23)	42.00 (0.00)	8.72 (1.07)
1989	1	1	0.034 (0.009)	0.262 (0.049)	3.8 (0.9)	2.13 (0.37)	54.13 (4.24)	54.23 (7.22)
	2	3	0.054 (0.007)	0.354 (0.031)	6.1 (1.1)	1.68 (0.14)	53.59 (1.97)	78.48 (7.53)
	5	1	0.022 (0.004)	0.163 (0.017)	2.2 (0.2)	1.64 (0.22)	61.02 (1.84)	93.11 (7.77)
	7	1	0.033 (0.010)	0.211 (0.039)	5.2 (1.9)	1.17 (0.11)	59.25 (2.27)	82.12 (6.38)
	8	1	0.008 (0.003)	0.068 (0.015)	1.2 (0.4)	1.21 (0.01)	66.58 (2.60)	84.00 (10.61)
	9	1	0.032 (0.014)	0.198 (0.040)	2.3 (1.0)	1.74 (0.32)	56.35 (6.70)	84.46 (11.24)
	10	3	0.012 (0.002)	0.095 (0.011)	2.5 (1.0)	1.29 (0.08)	64.76 (1.23)	82.22 (4.66)

[a] *RAUDPC*: relative area under the disease progress curve; *Yf*: final disease severity; *Ra*: absolute rate of disease increase derived from the Richards model; *m*: shape parameter derived from the Richards model; *DLF*: number of days from the beginning of the epidemic until leaf fall; *RHAD*: relative healthy area duration.

[b] Numbers in parenthesis represent standard errors of means.

Disease severity was estimated on each leaf individually as a proportion of the maximum number of uredia and telia (estimated at approximately 400) recorded in four fields of 1 cm^2 each (18). To compensate for loss of diseased tissue caused by leaf fall, cumulative disease severities (6) were calculated using a corrected equation for leaf fall:

$$x_t = \frac{X_{cut} + X_{fct}}{Y_{cut} + Y_{fct}}$$

in which x_t is the proportion of leaf area rusted, X_{cut} and Y_{cut} are diseased and total leaf areas at time t, and X_{fct} and Y_{fct} are cumulative diseased and total leaf areas removed by leaf fall.

Disease progress curves were generated by plotting disease severities against time for each tree and were characterized by computing the relative area under the disease progress curve (*RAUDPC*) (3,16), the final disease severity (*Yf*), and the absolute-rate (*Ra*) and shape (*m*) parameters from the Richards growth model (13). (*RAUDPC* was calculated instead of *AUDPC* to allow the comparison of epidemics between years).

In 1990, to allow sampling of a larger number of families, disease severities were recorded at one time only, on October 2, on the best predictor date for *RAUDPC* in 1988 and 1989, as reported in this article. Two leaves on each of two branches of each of 40 families were removed and brought to the lab, where disease severities were measured as in 1988 and 1989.

Defoliation. The number of days between the first observation and the time of leaf fall (*DLF*) was recorded for each of the previously tagged leaves. Total leaf area was approximated by comparing leaves with a pictorial key showing 20 drawings of leaves ranging from 50 to 250 cm^2. Diseased and removed tissue were subtracted from total leaf area to yield the healthy-area index (*HAI*) (22). The relative healthy-area duration (*RHAD*), a second variable of defoliation that may be more closely related to yield, was calculated by measuring the area under the *HAI* curves against time for the period of the rust season for each tree divided by the number of days of duration of the epidemic to allow for comparison between years. While *DLF* gave an indication of the time in days when defoliation took place, the *RHAD* represented the amount of healthy tissue (centimeters squared) present over the course of the epidemic.

In 1990, defoliation was measured as the proportion of fallen leaves from two branches per tree, estimated as the number of leaf scars on the current season's growth divided by the sum of the number of leaf scars and leaves present.

Statistical analysis. Parameters from the Richards model were estimated by using nonlinear regression procedures (PROC SYSNLIN) (9,14). The asymptote was fixed at the final disease severity, *Yf* (a fair assumption given that the epidemic was practically over at the time of the last disease measurement), and the intercept was restricted to provide realistic values of initial disease severity.

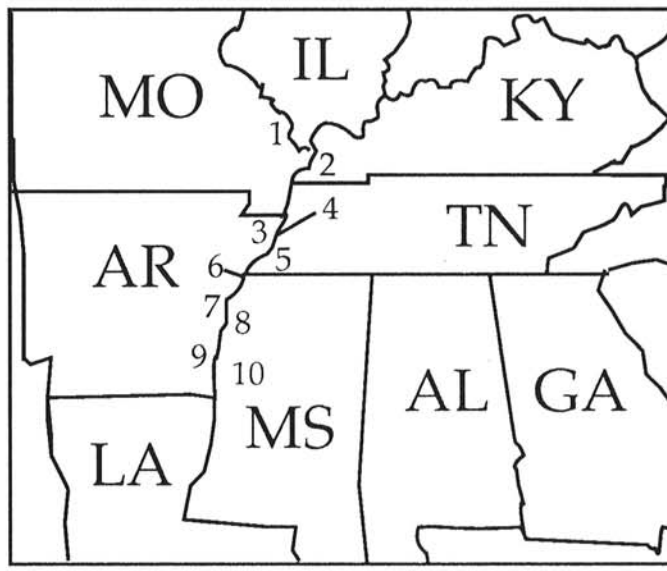

Fig. 1. Map of locations of origin of eastern cottonwood families.

Data for *RAUDPC, Yf, Ra, m, RHAD,* and *DLF* were subjected to an analysis of variance (ANOVA), and contrasts were used to compare northern (locations 1–5) and southern (locations 6–10) families. In 1990, an ANOVA was performed on disease severity and defoliation, with families nested within the location of origin.

To determine the best one- and two-observation predictor of cumulative disease severity for the entire season, the *RAUDPC* was regressed against disease severity at individual observations (e.g., *RAUDPC* vs. X_i) for each tree in 1988 and 1989. The best models were selected by using a stepwise regression procedure (PROC STEPWISE; best R^2 method) (14).

Relationships between disease progress and defoliation were investigated by calculating Pearson correlation coefficients between all variables in 1988 and 1989. A hierarchical cluster analysis, using the centroid method (PROC CLUSTER) (14), was performed on all six disease progress and defoliation variables in 1988 and 1989. The variables were averaged over each cluster to assess geographic trends.

RESULTS

Disease progress. The first uredia were observed on 18 August 1988 and 7 August 1989. The eastern cottonwood families varied widely with respect to the development of poplar leaf rust epidemics (Fig. 2).

In both years, the lowest *RAUDPC, Yf,* and *Ra* were recorded for families from locations 8 and 10, with the exception of *Ra* for families from location 10, which was the fourth lowest in 1989. The results indicate that the southern families were less susceptible to the local pathogen population at the test site than were their northern counterparts. Families from locations 1 and 2, which were derived from within a few miles of the test site, were among the most susceptible to local inoculum as indicated by the large values of *RAUDPC, Yf,* and *Ra* (Table 1).

The *RAUDPC* and *Ra* were generally lower in 1989 than in 1988, reflecting a more severe epidemic during 1988. Final disease severities (*Yf*) were similar for both years, however. The points of inflection of the disease progress curves generally were earlier in 1988 than in 1989, as indicated by the smaller values of *m* during the first year (Table 1). Values of *m* were within the range expected for polycyclic diseases ($m = 1$ for Gompertz and $m = 2$ for logistic) (13).

Based on results from the ANOVA, *RAUDPC, Yf,* and *Ra* were significantly higher in the northern than in the southern group of families during both seasons (Table 2). The *F*-test for *m* was only marginally significant ($P = 0.056$) in 1988 but was highly significant in 1989 ($P = 0.002$; Table 2).

Defoliation. Defoliation of susceptible trees occurred 3–4 wk after the beginning of the epidemic in 1988 as compared to 8 wk after in 1989. However, relative ranking of families for defoliation was similar in both years, with trees from locations 8 and 10 among the latest to defoliate and trees from locations 1 and 2 among the earliest (Table 1). In 1988, *RHAD* was larger in families from locations 8 and 10 than in the remaining families, by 71-fold; in 1989, there was only a slight difference among families derived from different locations. Families from northern locations had significantly ($P < 0.05$) earlier defoliation in both years compared to southern locations. The *RHAD* was significantly different in the two groups in 1988 but not in 1989 (Table 2).

One- and two-observation predictor of *RAUDPC*. Using a stepwise regression procedure, the dates on which disease severity (X_i, for the *i*th observation) best predicted *RAUDPC* (*Y*) included 28 September 1988 ($Y = 0.1780 + 32.90X_3$) ($R^2 = 0.99$) and 27 September 1989 ($Y = 0.2279 + 44.84X_4$) ($R^2 = 0.95$) for the one-observation model. In the two-observation model, the dates on which disease severity best predicted *Y* included 21 and 28 September 1988 ($Y = -0.2184 + 15.21X_2 + 20.53X_3$) ($R^2 = 0.99$) and 27 September and 5 October 1989 ($Y = 0.4832 + 172.34X_4 + 121.30X_5$) ($R^2 = 0.97$).

Disease severity and defoliation in 1990. There were significant differences in disease severities among the 40 families from 10 locations of origin in 1990 (Table 3). A north-south gradient was evident, with families from locations 1–4 having the highest disease severities, families from location 5 having intermediate severities, and families from locations 6–10 having the lowest severities. Defoliation also was affected by location of origin, with north-south separation once again apparent (i.e., families from locations 1 and 2 were significantly more defoliated than families from locations 3, 4, and 6–10) (Table 3).

Relationship between disease progress and defoliation. In 1988, *RAUDPC* was positively correlated with *Yf* and *Ra* (Table 4). Positive correlations also were found between *DLF* and *RHAD* and between *Yf* and *Ra*. The *RAUDPC* was negatively correlated with *DLF* and *RHAD*; in addition, weaker negative correlations were found between *DLF* and *Yf* and between *DLF* and *Ra*. No significant correlations were found between *m* and the remaining variables (*RAUDPC, Ra, DLF,* and *RHAD*). Correlations in 1989 were similar to those in 1988 except that *RHAD* was

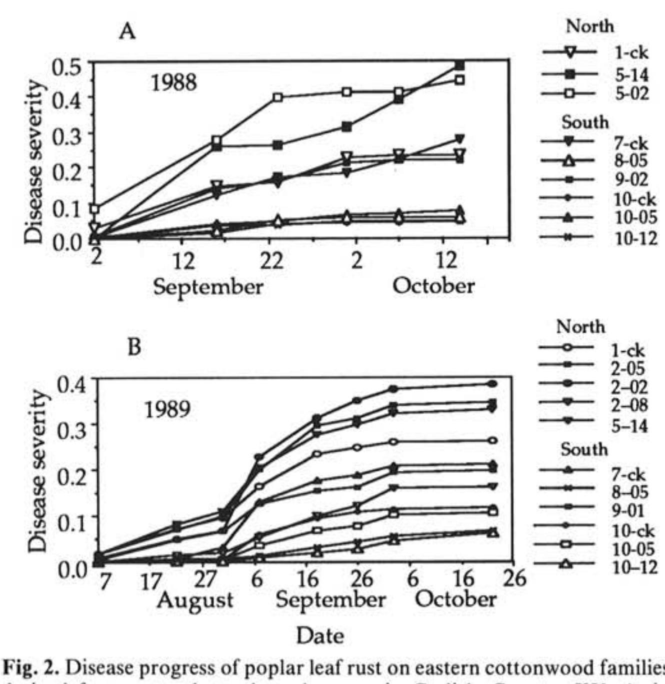

Fig. 2. Disease progress of poplar leaf rust on eastern cottonwood families derived from natural stands and grown in Carlisle County, KY, **A,** in 1988 and **B,** in 1989. Families are designated by their location of origin (e.g., family 10-05 is the fifth family from location 10). Families designated by "ck" were collected on a parent tree that could not be evaluated for rust resistance.

TABLE 2. Summary of contrast between families of eastern cottonwood derived from northern (1–5) and southern (6–10) locations for disease progress and defoliation variables of poplar leaf rust epidemics

	1988		1989	
Variable[a]	F[b]	$P > F$	F	$P > F$
RAUDPC	14.13	0.007	19.55	<0.001
Yf	8.73	0.021	23.93	<0.001
Ra	9.67	0.017	5.35	0.025
m	5.25	0.056	10.15	0.002
DLF	11.14	0.013	11.63	0.001
RHAD	8.15	0.025	0.89	0.350

[a] *RAUDPC*: relative area under the disease progress curve; *Yf*: final disease severity; *Ra*: absolute rate of disease increase derived from the Richards model; *m*: shape parameter derived from the Richards model; *DLF*: number of days from beginning of epidemic until leaf fall; *RHAD*: relative healthy area duration.

[b] *F*-test of the contrast of location of origin.

TABLE 3. Disease severity and defoliation caused by poplar leaf rust in 40 families of eastern cottonwood derived from natural stands at 10 locations along the Mississippi River valley and grown in Carlisle County, KY, in 1990

Location of origin	Disease severity[a]	Defoliation[b]
1	0.19 b[c]	0.66 a
2	0.30 a	0.67 a
3	0.22 b	0.52 bc
4	0.16 bc	0.49 bcd
5	0.11 cd	0.55 ab
6	0.06 d	0.36 d
7	0.06 d	0.50 bcd
8	0.04 d	0.36 d
9	0.05 d	0.37 cd
10	0.04 d	0.42 bcd

[a] Proportion of the maximum number of uredia and telia counted in four fields 1 cm^2 on two leaves on each of two branches per tree on 2 October.

[b] Proportion of fallen leaves estimated as the number of leaf scars on the new year's growth divided by the sum of the number of leaf scars and leaves present.

[c] Locations followed by the same letter within a column are not significantly different ($P = 0.05$; PLSD).

TABLE 4. Pearson correlation coefficient between epidemiological variables of poplar leaf rust on eastern cottonwood derived from natural stands along the Mississippi River valley and grown in Carlisle County, KY

	Variables[a]	*RAUDPC*	*Yf*	*Ra*	*m*	*DLF*	*RHAD*
1988	*RAUDPC*	1.000	0.863**[b]	0.915***	0.468	−0.868**	−0.903***
	Yf	...	1.000	0.965***	0.116	−0.711*	−0.747*
	Ra	...	...	1.000	0.256	−0.778*	−0.798**
	m	...	...	...	1.000	−0.480	−0.373
	DLF	...	...	...	...	1.000	0.975***
1989	*RAUDPC*	1.000	0.952***	0.772***	0.432***	−0.530***	−0.194
	Yf	...	1.000	0.789***	0.425***	−0.358**	−0.125
	Ra	...	...	1.000	0.052	−0.263*	−0.180
	m	...	...	...	1.000	0.404**	−0.067
	DLF	...	...	...	...	1.000	0.449***

[a] *RAUDPC*: relative area under the disease progress curve; *Yf*: final disease severity; *Ra*: absolute rate of disease increase derived from the Richards model; *m*: shape parameter derived from the Richards model; *DLF*: number of days from the beginning of the epidemic until leaf fall; *RHAD*: relative healthy area duration.

[b] *, ** and *** indicate that the Pearson correlation coefficient is significantly different from 0 at $P < 0.05$, 0.01, and 0.001, respectively.

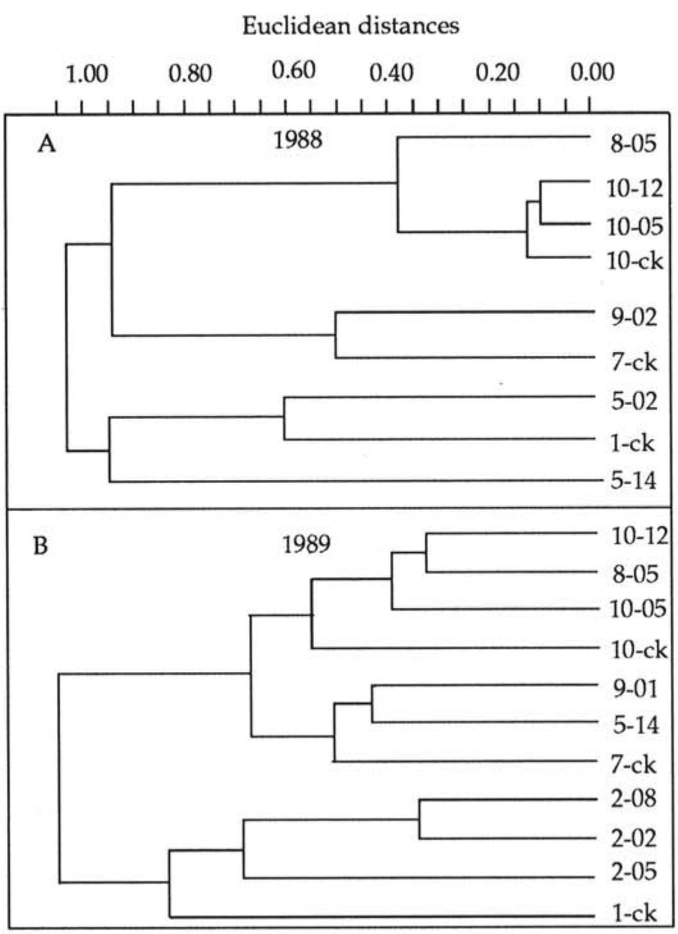

Fig. 3. Hierarchical cluster analysis of the disease progress and defoliation parameters for epidemics of poplar leaf rust on eastern cottonwood families derived from natural stands and grown in Carlisle County, KY, **A**, in 1988 and **B**, in 1989. Families are designated by their location of origin, (e.g., family 10-05 is the fifth family from location 10). Families designated by "ck" were collected on a parent tree that could not be evaluated for rust resistance.

not significantly correlated with any of the disease progress curve variables, whereas *m* was significantly correlated with *RAUDPC*, *Yf*, and *DLF* (Table 4).

Cluster analysis. In both years, families separated, approximately, into northern and southern clusters. In 1988, families seperated into one loose (locations 1, 5, 7, and 9) and one tight (locations 8 and 10) cluster (clusters 1 and 2, respectively) (Fig. 3A). Similarly, in 1989, families separated along geographical lines into two clusters, with families from locations 1 and 2 forming a northern cluster (cluster 1) and families from locations 5 and 7–10 forming a southern cluster (cluster 2) (Fig. 3B).

The average *RAUDPC*, *Yf*, and *Ra* in cluster 1 were approximately 2.5–5 times and 2–3 times larger than in cluster 2 in 1988 and 1989, respectively (Table 5). Also, *DLF* in cluster 1 was, on average, 15 days earlier in 1988 and 9 days earlier in 1989 than in cluster 2. The *RHAD* was 10 times smaller in cluster 1 than in cluster 2 in 1988 but was similar in size in both clusters in 1989. Larger values of *m* were observed in cluster 1 than in cluster 2 during both years.

DISCUSSION

Eastern cottonwood families derived from natural stands along the Mississippi River valley varied widely in their resistance to poplar leaf rust at the test site. North-south separation of the families was apparent during the three seasons included in this study; families derived from northern locations, closer to the test site, were more susceptible to the local pathogen population than those derived from southern locations.

Geographic variation in disease susceptibility has been reported previously in the poplar leaf rust-eastern cottenwood pathosystem. For example, Thielges and Adams (20) reported that *P. deltoides* families derived from Missouri and Illinois were more resistant than those from Ohio, Pennsylvania, and Indiana when grown in Ohio. Also, eastern cottonwood clones derived from northern natural stands in the Mississippi River valley at lat. 34°57′ N were more resistant to poplar leaf rust than those originating near Baton Rouge, LA (lat. 30°31′ N), when grown in Greenville, MS (1). It is notable that Cooper and Filer's (1) northernmost location of collection, corresponding to our southernmost location, produced the most susceptible clones when tested in Greenville, MS, yet *P. deltoides* families derived from approximately the same location and grown in Carlisle County, KY, were the most resistant to poplar leaf rust in our study. Thielges and Adams' (20) southernmost and most resistant families corresponded geographically to our northernmost and most susceptible families.

Based on these results, we suggest that the pathogen specializes on local host genotypes. Pathogenic variation has been reported for poplar leaf rust in North America (11, 12) and in northwestern Europe (10). In the latter case, pathogenic specialization coincided with geographic location of testing: Clone Unal, grown in the Netherlands, was completely free of rust until 1982 despite epidemics on other clones, while the same clone was susceptible at Orléans, France.

Using a leaf-disk assay, clone ST75 from Stoneville, MS, was highly resistant to inoculum from Lexington, KY, but susceptible to inoculum from Stoneville (L. Shain, *unpublished*). Also, pathogen isolates of southern origin were better adapted to cottonwood clones derived from the same location, and isolates of northern origin were less adapted to southern host material (4). These reports and the results communicated here support the hypothesis that poplar leaf rust is locally adapted to eastern cottonwood.

All epidemiological variables measured, with the exception of *Yf*, indicate that a more severe epidemic occurred in 1988, despite

TABLE 5. Disease progress and defoliation variables for epidemics of poplar leaf rust on eastern cottonwood derived from natural stands along the Mississippi River valley and grown in Carlisle County, KY

	Cluster[b]	Disease progress and defoliation variables[a]					
		RAUDPC	*Yf*	*Ra* ($\times 10^{-3}$)	*m*	*DLF* (days)	RHAD ($\times 10^{3}$)
1988	1	0.245	0.385	8.5	2.48	27.35	0.39
	2	0.046	0.071	3.4	1.17	42.00	3.32
1989	1	0.046	0.331	5.5	1.79	53.74	7.27
	2	0.017	0.132	2.6	1.38	62.50	8.43

[a] *RAUDPC*: relative area under the disease progress curve; *Yf*: final disease severity; *Ra*: absolute rate of disease increase derived from the Richards model; *m*: shape parameter derived from the Richards model; *DLF*: number of days from the beginning of the epidemic until leaf fall; *RHAD*: relative healthy area duration.

[b] In 1988, cluster 1 comprised families from locations 1, 5, 7, and 9, and cluster 2 comprised families from locations 8 and 10; in 1989 cluster 1 comprised families from locations 1 and 2, and cluster 2 comprised families from locations 5 and 7–10.

the severe drought that affected the Mississippi River valley, than occurred in 1989. This result supports an earlier report that low precipitation is not a factor limiting poplar leaf rust epidemics in the Mississippi River valley (4).

Based on the significant difference in the Richards shape parameter between families from different locations, the shape can depend on the location of host origin. The lower values of *m* for resistant families indicate that the point of inflection of the disease progress curve occurs earlier in the epidemic than it occurs for susceptible families (13).

The highly significant correlations between disease progress curve variables are not surprising because many are conceptually interrelated. Nevertheless, the lack of correlation between *m* and *Ra* indicates that the Richards model is not overparameterized, and the shape parameter provides nonredundant information about the epidemics.

The significant negative relationship between disease progress variables and the time of defoliation confirms the causality of the disease on early defoliation. This relationship was also evident when a multiple regression analysis was performed with the location of origin as an independent variable, indicating that disease severity, independant of location of origin, accounts for the large differences in defoliation dates (R. C. Hamelin, *unpublished*).

One disease measurement on 28 September 1988 and 27 September 1989 was sufficient to account for 99 and 95% of the variation in *RAUDPC*, respectively. This result strongly suggests that, for a quick evaluation of eastern cottonwood genotypes for rust resistance in western Kentucky, one observation during the last week of September or the first week of October would account for most of the variation over the season.

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