Variability in Aggressiveness, Recovery, and Cultural Characteristics of Isolates of Ceratocystis ulmi

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ABSTRACT

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Seedlings of several elm species were inoculated with isolates of *Ceratocystis ulmi* from various geographic areas in the United States. The isolates caused different amounts of foliar and vascular symptoms regardless of seedling species, age, or the environment. The more aggressive isolates were recovered from *Ulmus pumila* more frequently than the less aggressive ones, but all were recovered with about equal frequency from *U. americana*. With some exceptions, the more aggressive isolates grew more rapidly on agar media, were intermediate in mycelial habit between appressed and fluffy, and produced more coremia on wood of both *U. americana* and *U. pumila*.

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Elms susceptible to the Dutch elm disease (DED) occur extensively throughout the United States. Differences in the severity of disease symptoms, frequency of infection and rate of decline of infected trees have been attributed to variability in host resistance or environment. Little attention has been given to the occurrence of strains of the causal fungus, *Ceratocystis ulmi* (Buism.) C. Moreau, that vary in aggressiveness. Buisman (1) mentioned differences in pathogenicity in Europe, but did not elaborate. Tyler and Parker (7) found nonsignificant variation in pathogenicity among eight *C. ulmi* isolates from two sites in New York State. Holmes (4) found ascospore cultures from a single cross varied in virulence in young elms in the greenhouse. In Britain, Gibbs et al. (3) noted a fungus strain that was more aggressive (8) than any previously found. Holmes et al. (5) confirmed that the British isolates associated with rhe resurgence of DED in Britain were more aggressive than those from the Netherlands.

Variability in cultural characteristics of *C. ulmi* has been reported by Swingle (6) and Walter (9), but was not related to differences in aggressiveness. Gibbs and Brasier (2) correlated cultural characteristics of their isolates with aggressiveness.

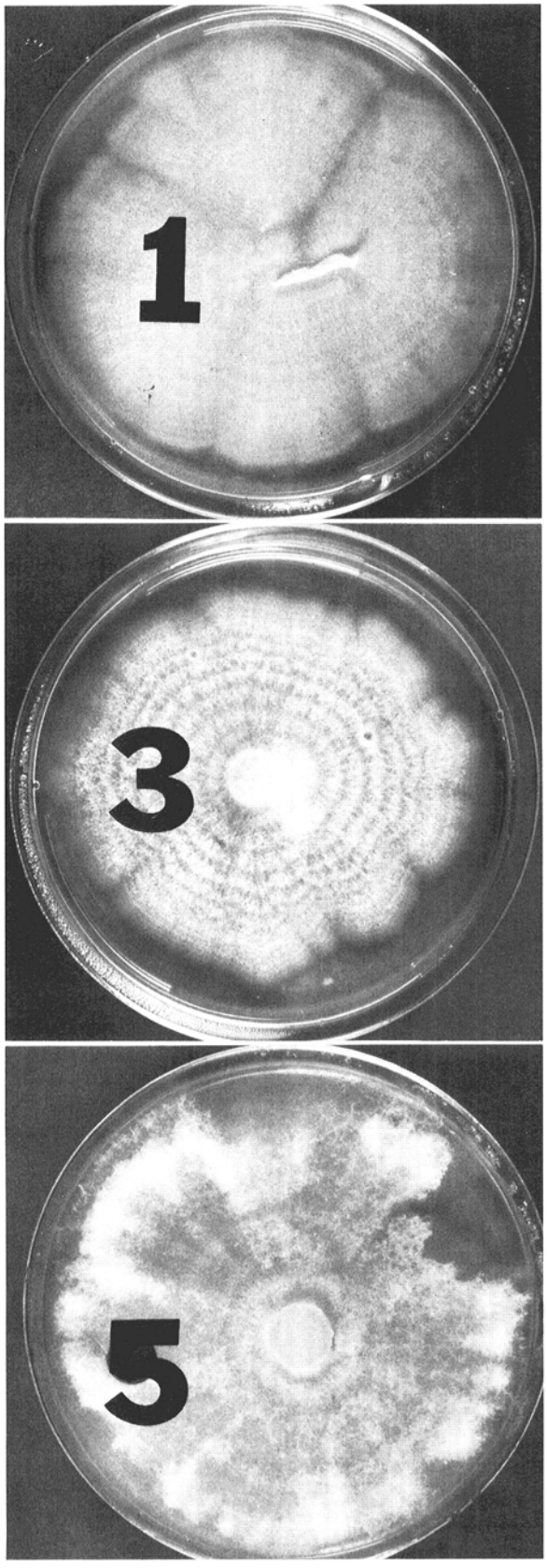
In this study, we evaluated variability in aggressiveness of *C. ulmi* isolates from various parts of the United States and correlated differences with cultural characteristics, rate and extent of colonization, and recovery of the fungus from host plants.

MATERIALS AND METHODS

Variability in isolate aggressiveness and recovery.—Five *C. ulmi* isolates that had been in culture for 3 years or more, from North Carolina (NC), Ohio (OH), North Dakota (ND), Colorado (CO-FM), and Massachusetts (MA-B) were inoculated into 10- to 12-year-old American elms, *Ulmus americana* L., and reisolated after symptom expression. Reisolated cultures were grown in potato-dextrose broth (PDB) on a rotary shaker for 3 days at 25.5 C. On June 1972, 0.1 ml of a standardized spore suspension (1×10^6 spores/ml) of each isolate was inoculated into the trunks of each of 10 *U. americana* and 10 *U. pumila* through a 5 mm-wide chisel wound 15 cm above the ground. Treatments were completely randomized within each species. The percentage of the crown with symptomatic foliage was considered a measure of aggressiveness and was determined by observations on 23 June, 14 July, and 4 August, 1972, and 13 June 1973.

The presence of the isolates was determined by sampling inoculated trees on 10 July 1972. Three spores, 5 × 20 mm, were removed with an increment hammer from equidistant points around the trunk 240 cm above the ground, and placed on acidified potato-dextrose agar (PDA). Presence of *C. ulmi* was determined after 7 days. Recovery of each isolate was expressed as a percent of increment cores and as a percent of trees in which the isolate was detected.

Ceratocystis ulmi was isolated from branch samples of American elm received from Missouri (MO), Illinois (IL), Tennessee (TN), Virginia (VA), Alabama (AL), Colorado (CO-D), Massachusetts (MA-N), Iowa (IA), Maine (ME), and Wisconsin (WI) and the aggressiveness of each isolate was determined as described above. Fifteen 10- to 12-year-old *U. americana* and *U. pumila* were inoculated on 6 June or 17 May 1973, respectively, with each isolate. The ND and MA-B isolates, whose aggressiveness had been previously determined, were used as standards. Recovery of *C. ulmi* from trees inoculated with three of the most and three of the least aggressive isolates was



attempted by sampling on 23 June 1973, as described above.

Aggressiveness in relation to cultural characteristics.—Linear growth rate, coremia and pigment production, and mycelial habit were determined for 16 isolates.

Isolates were grown 2-3 days in petri plates on PDA. Disks 1 cm in diameter were cut from the edge of the colony and placed in the center of petri plates containing malt extract agar (MEA) (20g Bacto-Agar; 40g malt extract/liter), or PDA. Ten plates of each medium were inoculated with each isolate and incubated in the dark at 25 C. The diameters of colonies on MEA and PDA were measured after 11 and 5 days, respectively.

After 20 days of growth on PDA and MEA, the mycelial habit of the isolates was rated from 1 (appressed or yeastlike) to 5 (aerial or fluffy mycelia) (Fig. 1). Pigmentation was noted.

We compared the numbers of coremia produced by each isolate on disks, of *U. americana* and *U. pumila* wood, 1.0-1.5 cm in diameter and 1 cm thick. Disks were surface-sterilized by alcohol flaming and placed on acidified PDA, with three disks per plate and five plates per isolate per elm species. Each disk was inoculated with 0.1 ml of a standardized spore suspension and incubated in the dark at 24 C for 7 days. Coremia in two standard-areas per disk were counted.

Fungus distribution and vascular browning.—Fungus distribution immediately after inoculation was determined for the CO-FM, OH, MA-B, NC, and ND isolates in 5-month-old seedlings of *U. americana, U. pumila,* smooth-leaved (*U. carpinifolia* Gleditsch.), or Scotch elm (*U. glabra* Huds.). Seedlings were grown in the greenhouse in a medium of peat, perlite, and soil (2:2:1, v/v) under a 16-hour photoperiod. Intact roots of 10 seedlings of each elm species were immersed in a standardized spore suspension of each isolate for 18 hours at 25 C. To determine fungus distribution, we plated 2.5-cm sections from each third of the stem onto acidified PDA.

We determined differences between isolates in initial spore movement in the transpiration stream and later differential growth rates. In the greenhouse, each of five groups of 20 3-year-old *U. pumila* seedlings was inoculated with 0.1 ml of a standardized spore suspension of one of the five isolates used above. The spores were introduced into a 5 mm-wide wound at the base of the stem. The plants were arranged in a completely randomized design. Twenty-four hours after inoculation, 10 seedlings from each treatment were harvested, and 2.5-cm sections from the top of each quarter of the stem were plated on acidified PDA. The presence of vascular browning (VB) and viable fungus (VF) was noted for each section. After 21 days, VB and VF distribution was determined as described from a section from each tenth of the stem of 10 remaining trees.

To determine coincidence of VB and VF and their rates

Fig. 1. Visual rating scale for variations in mycelial growth habit of *Ceratocystis ulmi* isolates on 2% potato-dextrose agar: 1 = appressed to agar; 3 = intermediate between appressed and aerial; and 5 = aerial or fluffy.

TABLE 1. Percentage of crown symptoms on and isolation from 10- to 12-year-old *Ulmus americana* and *U. pumila* seedlings at various times after inoculation with isolates of *Ceratocystis ulmi*

Exp. no. and isolates	*U. americana*						*U. pumila*					
	Crown symptoms (%)				% Isolation from:[a]		Crown symptoms (%)				% Isolation from:	
					Increments	Trees					Increments	Trees
Experiment I[b]:												
	23 Jun 72	14 Jul 72	4 Aug 72	13 Jun 73			23 Jun 72	14 Jul 72	4 Aug 72	13 Jun 73		
CO-FM	27 w[c]	61 x	67 x	85 w	100 w	100 w	0 w	7 x	4 x	0 x	7 x	20 x
MA-B	21 w	43 y	57 x	83 w	90 w	100 w	0 w	6 x	5 x	1 x	23 w	30 x
NC	28 w	52 xy	65 x	98 w	70 x	80 w	0 w	2 x	1 x	0 x	13 x	30 x
ND	27 w	89 w	89 w	100 w	87 w	100 w	4 w	37 w	33 w	10 w	30 w	70 w
OH	16 x	55 xy	67 x	92 w	63 x	80 w	0 w	2 x	2 x	0 x	10 x	20 x
Experiment II[d]:												
	5 Jul 73	16 Aug 73	20 Jun 74				12 Jun 73	16 Aug 73	20 Jun 74			
AL	62 w	89 w	100 w		87 w	100 w	47 w	14 w	11 w		49 w	73 w
CO-D	50 wx	81 w	100 w		89 w	100 w	46 w	20 w	10 w		53 w	87 w
IA	59 w	74 wx	100 w				34 w	12 w	19 w			
IL	49 wx	78 w	100 w				46 w	11 w	15 w			
MA-B	24 yz	35 y	65 x		98 w	100 w	2 x	1 x	1 y		18 x	53 x
MA-N	18 z	39 y	75 x		91 w	100 w	6 x	2 x	1 y		11 xy	27 y
ME	36 xy	62 x	87 w				44 w	22 w	14 w			
MO	49 wx	74 wx	98 w				36 w	18 w	13 w			
ND	60 w	89 w	100 w		91 w	100 w	42 w	12 w	7 wx		49 w	87 w
TN	20 z	33 y	49 y		93 w	100 w	0 x	0 x	0 y		4 y	7 z
VA	54 w	79 w	99 w				39 w	14 w	11 w			
WI	55 w	85 w	99 w				39 w	9 w	4 xy			

[a]Isolations were made on 10 July 72 in Experiment I and on 23 June 73 in Experiment II.
[b]Ten *U. americana* and *U. pumila* seedlings were inoculated 9 June 72.
[c]Within experiments, means in a column followed by the same letter do not differ significantly at $P = 0.05$.
[d]Fifteen *U. americana* and *U. pumila* seedlings were inoculated on 6 June and 17 May 73, respectively.

TABLE 2. Growth rate, mycelial habit, and pigment production on potato-dextrose agar (PDA) and malt extract agar (MEA) and coremia production on *Ulmus americana* and *U. pumila* wood disks of isolates of *Ceratocystis ulmi*

Isolate	PDA		MEA		Av. No. coremia/disk	
	Diam growth (mm)	Mycelial habit[a]	Diam growth (mm)	Mycelial habit	*U. americana*	*U. pumila*
AL	72 tu[b]	3.0	60 tu	1.1	130 uv	93 u
CO-D	66 tuv	3.2	57 uv	1.1	135 uv	18 wx
CO-FM	57 w	3.8	59 tu	1.0	0 z	0 y
IL	70 tu	3.0	62 t	1.0	87 w	66 v
IA	68 tu	3.0	58 uv	1.0	182 t	137 t
MA-B	59 vw	5.0	47 y	1.0	0 z	0 z
MA-N	65 uv	2.8	55 vw	1.0	60 x	4 x
ME	47 y	1.0	45 y	1.0	130 uv	108 u
MO	73 t	3.1	58 uv	1.0	107 vw	28 w
NC	48 xy	1.1	49 x	1.0	0 z	0 y
ND	70 tu	3.1	60 tu	1.2	155 tu	155 t
NY	65 uv	2.9 (P)[c]	53 w	1.0	78 w	. . .
OH	53 wx	2.5 (P)	40 z	1.0 (P)	50 x	2 x
TN	46 y	1.1	47 xy	1.0	18 y	16 wx
VA	. . .	. . .	. . .	. . .	95 w	102 v
WI	67 uv	3.2	59 tu	1.0	127 v	88 v

[a]Mycelial growth habit was rated on a scale ranging from: 1 = appressed to agar with yeast like growth; to 3 = intermediate between appressed and aerial; and to 5 = fluffy or aerial growth.
[b]Means in a column followed by the same letter do not differ statistically at $P = 0.05$.
[c]Mycelium is pigmented.

of movement in stems of 3-year-old ramets of a clone each of *U. pumila* and *U. carpinifolia* and 3-year-old seedlings of *U. pumila* in the greenhouse, we inoculated them with the five isolates used above. Fifteen seedlings and seven ramets of *U. pumila* and eight ramets of *U. carpinifolia* were inoculated with each isolate. After 9 weeks, the *U. pumila* seedlings were harvested, and the linear extent of discoloration was determined for each isolate as percentage of the total stem height. The ramets of *U. pumila* and *U. carpinifolia* were harvested after 10 and 6 weeks, respectively. VB and VF were determined in the top 2.5-cm section of each quarter of the stems. Coincidence of VB with VF was defined as a percentage of discolored sections that contained the fungus. Coincidence of VF and VB was defined as percentage of sections containing the fungus that were discolored.

RESULTS

Variability in isolate aggressiveness and recovery.—*Ceratocystis ulmi* isolates varied in the percent of crowned symptoms they produced in *U. pumila* and *U. americana*. The more aggressive isolates were recovered more often from *U. pumila* than less aggressive ones. The ND isolate caused significantly more crown symptoms on both *U. pumila* and *U. americana* five weeks and eight weeks after inoculation than did the other four isolates. One year after inoculation, the highest percentage of crown symptoms again occurred in *U. pumila* inoculated with the ND isolate. Crown symptoms in all *U. americana* had increased over the percentage on the last reading date in the year of inoculation so that differences between isolates were no longer significant. All isolates were recovered from 80 - 100% of *U. americana* with no significant differences among isolates. The ND isolate was recovered from 70% of *U. pumila*, whereas the other four isolates were recovered from 20 to 30% of the trees. Also, the ND isolate was recovered from the highest percentage of stem increments from *U. pumila* (Table 1, Experiment I).

Inoculation of the 12 isolates into *U. americana* and *U. pumila* in 1973 resulted in significant differences in the percentage of crown symptoms. The frequency of recovery of three of the most and three of the least aggressive isolates are given in Table 1, Experiment II. Isolates most aggressive in *U. americana* were most aggressive in *U. pumila* and those least aggressive in *U. americana* were, likewise, least aggressive in *U. pumila*. Isolates from Massachusetts (MA) and Tennessee (TN), were significantly less aggressive than the others. The Maine (ME) isolate was intermediate in aggressiveness on *U. americana*. Differences in isolate aggressiveness were also reflected in the percentage of *U. americana* with less than 25% symptoms in 1974. For MA-B, TN, MA-N, and ME, these were 33, 47, 13, and 13%, respectively. All trees inoculated with any other isolates displayed more than 25% crown symptoms.

The more aggressive isolates were recovered from *U. pumila* significantly more often than were the less aggressive ones. Among the less aggressive, the TN isolate was recovered significantly less often than MA-B or MA-N. All isolates were recovered with about equal frequency from *U. americana*.

Aggressiveness in relation to cultural characteristics.—In general, the more aggressive isolates were faster growing, intermediate in mycelial habit between fluffy and appressed, and produced more coremia than less aggressive ones. The least aggressive isolates were the slowest growing on both MEA and PDA, whereas most of the more aggressive ones grew more rapidly (Table 2).

The mycelial habit of all isolates on MEA was appressed and yeastlike. The mycelial habit of isolates on PDA varied widely. The least aggressive isolates ranged in habit from appressed (TN, NC) to fluffy (MA-B), but the most aggressive ones were intermediate. The ME isolate, rated intermediate in aggressiveness, had the most appressed growth. The OH isolate produced pigmented mycelia on both MEA and PDA; the NY isolate was pigmented only on PDA.

The least aggressive isolates produced few or no coremia on wood disks of either *U. americana* or *U. pumila*. The most aggressive generally produced the greatest number of coremia. Aggressive isolate CO-FM did not produce coremia on wood of either species, while CO-D and MO produced as few coremia on *U. pumila* wood as less aggressive ones. Most isolates produced somewhat fewer coremia on *U. pumila* than on *U. americana* elm wood disks; CO-D, MO, MA-N, and OH produced far fewer.

Fungus distribution and vascular browning.—Distribution of the five isolates was similar in all species within 24 hours after root or stem inoculation. Isolates did not differ significantly in frequency of recovery from *U. americana, U. carpinifolia, U. pumila*, or *U. glabra* after root inoculation. However, *C. ulmi* was reisolated significantly more often from the top third of *U. americana* and *U. pumila* than from the top third of the other two species. Twenty-four hours after stem inoculation, there were no significant differences in the percentages of stem sections of 3-year-old *U. pumila* showing VB or VF. Vascular browning (VB) and VF were confined mainly to the bottom of the stem, occurring in 100 and in 20-50% respectively of bottom sections. Some discoloration appeared in the third quarter of the stem, but VF was confined to the bottom quarter.

After 21 days, there were significant differences between isolates in distribution of VB and VF. The ND isolate was reisolated from, and produced discoloration in significantly more stem sections than did other isolates. Isolates OH, NC, and MA-B produced the least discoloration and the lowest percentages of fungus reisolation, and CO-FM was intermediate. VB produced by the ND isolate was uniformly distributed along the length of the stem, whereas the other isolates produced decreasing discoloration from the point of inoculation to the top. The ND isolate was present in all stem sections, but was more often recovered from the upper two-thirds of the stem. The other isolates were more often recovered from the upper half of the stem (Table 3).

Nine weeks after inoculation of *U. pumila* seedlings, the percentage of the total stem length with VB caused by the ND isolate (89%) was significantly greater than the percentages produced by the other four isolates. Isolates CO-FM, OH, MA-B, and NC caused VB in 70, 63, 50, and 56% of stem sections, respectively.

TABLE 3. Number of stem sections with signs of viable fungus (VF) and vascular browning (VB) symptoms from 10 3-year-old *Ulmus pumila* 21 days after inoculation with different isolates of *Ceratocystis ulmi*

Isolates	Symptom or sign	Stem sections										
		Top	2nd	3rd	4th	5th	6th	7th	8th	9th	Bottom	Av
CO-FM	VB	3	3	5	6	6	7	9	9	8	9	6.5 b[a]
	VF	1	3	3	1	3	0	0	0	1	1	1.3 b
OH	VB	2	2	4	5	6	7	8	8	8	9	5.9 b
	VF	0	0	1	2	4	2	0	0	0	0	0.9 b
MA-B	VB	1	2	3	3	4	5	4	4	5	7	3.8 c
	VF	1	2	3	0	0	0	1	0	0	0	0.7 b
ND	VB	9	9	9	9	9	9	9	10	10	10	9.3 a
	VF	6	6	7	9	9	7	4	6	4	4	6.2 a
NC	VB	1	2	5	5	5	6	8	8	9	10	5.9 b
	VF	0	0	1	2	0	0	0	1	0	0	0.4 b

[a]Values followed by the same letter in the Av column for each parameter (VB or VF) do not differ significantly at $P = 0.05$.

TABLE 4. Percentage of stem sections with vascular browning (VB) and viable fungus (VF) and coincidence between VB and VF in *Ulmus pumila* and *U. carpinifolia* ramets inoculated with isolates of *Ceratocystis ulmi*

Ulmus sp. and *C. ulmi* isolates	Stem sections with VB (%)	Stem sections with VF (%)	Stem sections with VF that show VB (%)	Stem sections with VB that contain VF (%)
U. pumila				
ND	72 x[a]	22 x	100	29
OH	46 yz	7 y	50	8
CO-FM	57 y	0 y	. . .	. . .
NC	36 z	0 y	. . .	0
MA-B	46 yz	5 y	100	7
U. carpinifolia				
ND	89 x	22 x	100	21
OH	92 x	7 y	100	8
CO-FM	82 x	16 x	100	19
NC	75 x	0 y	. . .	0
MA-B	85 x	25 x	67	26

[a]Means in a column followed by the same letter do not differ significantly at $P = 0.05$.

Vascular browning (VB) and VF produced by the five *C. ulmi* isolates varied with the elm species. In *U. pumila* ramets, the ND isolate produced the most VB and VF. The percentage of recovery did not differ significantly for the other isolates. In *U. carpinifolia* ramets, isolates did not cause significant differences in percentages of VB. The ND, CO-FM, and MA-B isolates were recovered most often from this species. Viable fungus (VF) appeared in 9% of the discolored stem sections of *U. pumila* and in 15% of those of *U. carpinifolia* ramets. The highest correlation was 29% in *U. pumila* inoculated with the ND isolate. The percent of stem sections of *U. pumila* and *U. carpinifolia* with VF that were discolored were 83 and 92%, respectively. There were no significant differences between isolates (Table 4).

DISCUSSION

We have shown that *C. ulmi* isolates from diverse geographic areas in the United States vary greatly in aggressiveness. Most of our isolates were highly aggressive pathogens, a few were weak pathogens, and one, from Maine (ME), was intermediate. Both isolates from Massachusetts were weak pathogens. The occurrence of less aggressive isolates in New England may be related to the apparently less severe occurrence of Dutch elm disease there.

In *U. americana,* our less aggressive isolates caused slower development of foliar symptoms, so there were greater differences among isolates in the year of inoculation than the next year. Also, data from the year after inoculation indicate significantly better chances of survival of *U. americana* inoculated with the less aggressive isolates: 13-47% of trees inoculated with these showed less than 25% crown symptoms, but all trees inoculated with the more aggressive isolates showed higher percentages.

We found no specificity in aggressiveness of any of the

isolates for any elm species. The most pronounced differences in aggressiveness were noted among isolates in 10- to 12-year-old *U. pumila* or *U. americana*. The apparent lack of differences among isolates in *U. carpinifolia* or *U. glabra* is attributed to the general scarcity of crown symptoms in most elms less than 3 years old in a greenhouse. When symptoms did appear in the greenhouse, they were produced by the same isolates that were most aggressive in the field in older elms. In addition, isolates that had been carried in culture for 3 or more years were as aggressive as any isolated from diseased wood 9-10 months before our studies. None of the isolates declined in aggressiveness while in culture during the 3 years of this study. These results agree with those of Tyler and Parker, who also found the aggressiveness of *C. ulmi* to be stable in culture (7). The relative aggressiveness of isolates was constant in several elm species varying in age from 3 to 12 years old and in studies in diverse environments of the greenhouse and nursery. Thus, aggressiveness appears to be under strong genetic control.

Aggressive and nonaggressive isolates were both recovered with high frequency from *U. americana*. We found a positive correlation between aggressiveness and recovery of different isolates from *U. pumila*. The more aggressive isolates were recovered more often from a higher percentage of trees and from core samples from the trunk. All isolates were recovered from 20-50% of "Bottom" stem sections 24 hours after inoculation but only the two most aggressive isolates could be recovered from "Bottom" stem sections 21 days after inoculation. In addition, the more aggressive isolates were distributed in all sections along the length of the stem of *U. pumila* 3 weeks after inoculation. The less aggressive isolates were recovered mainly in the upper halves of the stems, but less frequently in these sections than were the more aggressive ones. These data indicate that the less aggressive isolates myltiply and grow more slowly and lose viability faster than do the more aggressive ones. Also, VB develops in advance of fungus growth in any part of the stem. Viable fungus (VF) was seldom found in the absence of VB in either *U. carpinifolia* or *U. pumila*, but VB often occurred where VF was absent.

Attempts to correlate aggressiveness and cultural characteristics were inconclusive. General trends indicated that the more aggressive isolates grew faster, were intermediate in mycelial habit between appressed and fluffy, and produced more coremia on wood of both *U. americana* and *U. pumila*. However, exceptions precluded an all-inclusive relationship between aggressiveness and any of the cultural characteristics. We were unable to correlate aggressiveness with mycelial habit as did Gibbs and Brasier (2). Growth rates of all isolates on PDA were slightly faster than on MEA but relative to one another, were similar on the two media. While most isolates produced more coremia on *U. americana* than on *U. pumila* wood, the relative order of isolates in coremia production was similar with two notable exceptions: The CO-D and MO isolates, both highly aggressive, produced as many coremia on *U. americana* wood as did equally aggressive isolates but fewer coremia on *U. pumila* wood than did other less aggressive ones.

Wide variability in aggressiveness among *C. ulmi* isolates poses potential problems for any program of disease control through host resistance. It has been previously assumed that pathogenic variability was extremely limited and even nonexistent in certain countries (H. M. Heybroek, *personal communication*). This study and studies of Gibbs et al. (3) and Holmes et al. (4) have shown that this variability is more extensive than previously thought and may be increasing. If these conclusions are valid, more extensive and careful screening will be warranted for disease-resistant elms.

LITERATURE CITED

1. BUISMAN, C. 1932. Ceratostomella ulmi, de geschlachtelijke vorm van Graphium ulmi Schwarz. Tijdschr. Plantenzkten 38:1-5.
2. GIBBS, J. N., and C. M. BRASIER. 1973. Correlation between cultural characters and pathogenicity of Ceratocystis ulmi from Britain, Europe and America. Nature 241(5389):381-383.
3. GIBBS, J. N., H. M. HEYBROEK, and F. W. HOLMES. 1972. Aggressive strain of Ceratocystis ulmi in Britain. Nature 236:121-122.
4. HOLMES, F. W. 1965. Virulence in Ceratocystis ulmi. Neth. J. Plant Pathol. 71:97-112.
5. HOLMES, F. W., H. M. HEYBROEK, and J. N. GIBBS. 1972. Aggressiveness of Ceratocystis ulmi. Phytopathology 62:939-940.
6. SWINGLE, R. U. 1936. A preliminary note on sexuality of the fungus Ceratostomella ulmi. Phytopathology 26:925-927.
7. TYLER, L. J., and K. G. PARKER. 1945. Pathogenicity of the Dutch elm disease fungus. Phytopathology 35:257-261.
8. VAN DER PLANK, J. E. 1968. Disease resistance in plants. Academic Press, New York. 206 p.
9. WALTER, J. M. 1937. Variation in mass isolates and monoconidium progenies of Ceratocystis ulmi. J. Agric. Res. 54:509-523.