Influence of Moisture, Temperature, Leaf Maturity, and Host Genotype on Infection of Elms by *Stegophora ulmea*

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ABSTRACT

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The influence of environmental and host factors on the initiation and development of black spot disease on both resistant and susceptible elm clones was investigated. Optimum disease development occurred when plants were exposed to 100% relative humidity at 16 C for 24 hr following inoculation with 10^6 spores per milliliter of conidial suspension. Low temperatures (12–16 C) resulted in increased disease incidence in moderately susceptible clones but did not have a significant effect on a highly susceptible clone of *Ulmus laevis*. Temperature did not influence the type (sporulating vs nonsporulating) of lesion present. Young, growing leaves were most susceptible; no lesions were found on leaves below the third internode from the growing tip. Repeatability estimates were high (0.88–0.91), which suggests a high heritability for clonal response to *S. ulmea* and a good potential for breeding and selection for resistance.

Stegophora ulmea (Schw.:Fries) Sydow and Sydow (= *Gnomonia ulmea* Schw.:Thum.) causal agent of black spot disease of elm, produces lesions on leaves, seeds, and shoots in many *Ulmus* species (13,20). Symptoms of the disease first appear in the spring as small chlorotic spots on the upper surface of young leaves. Within several days, the center of the spot darkens and becomes slightly raised. As the season progresses, necrotic tissue may develop around the original spot and several to many spots may coalesce, causing premature leaf abscission. The initial infection of leaves in the spring is caused both by ascospores produced in perithecia in overwintered leaves and by an unidentified source of inoculum (probably within the dormant buds) which results in severe infection of new leaves (5,12).

Two imperfect spore forms of *S. ulmea* have been identified (12,13,15). Macroconidia (*Gloeosporium ulmicolum* Miles) act as secondary inoculum as long as susceptible host tissue is available. The role of microconidia [*Gloeosporium ulmeum* Miles or *Cylindrosporella ulmea* (Miles) von Arx], which are produced in later summer, is still unknown, but it has been suggested that they may serve as spermatia (12,15).

Prior to the outbreak of Dutch elm disease caused by *Cerotocystis ulmi* (Buism.) C. Moreau, black spot was considered to be a major disease of elms, especially in nurseries (11), and several chemical controls were investigated and recommended (2–5,11,21). Black spot not only affects the vigor of susceptible trees but can also seriously detract from their aesthetic value. Currently the importance of black spot is limited because there is little commercial propagation of elms. However, since several clones resistant to Dutch elm disease have been released (8,17–19), the impact of black spot may soon be evident in commercial nurseries and landscape plantings unless potential releases are screened for black spot resistance.

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The factors involved in establishing the pathogen on a host for screening purposes have not been reported. Inoculations were attempted by Miles (14), Pomerleau (16), and Morgan-Jones (15). Miles (14) was able to reproduce symptoms in the field on the inoculated leaves of one shoot covered with an Ehrlenmeyer flask. Pomerleau (16) reported limited success with this method and inconsistent results when he exposed plants to several different environments after inoculation. Morgan-Jones (15) obtained a limited number of lesions on plants that had been incubated in a moist chamber for 48 hr following inoculation.

The importance of environmental factors in determining the severity of black spot disease in the field was investigated by Pomerleau (16). He found that lesion frequency increased 2–3 wk after a wet period. Although he suggested that temperature might be an important variable in disease spread, the temperatures in Quebec did not fluctuate sufficiently to influence disease incidence.

The following study was designed to determine the effect of moisture, temperature, and leaf maturity on the initiation and development of black spot disease. Knowledge of these factors is considered to be of major importance in the development of a controlled environment screening procedure. Also, because screening is useful in a breeding program only if host susceptibility is under genetic control, the results of these experiments were used to estimate heritability through a repeatability analysis.

MATERIALS AND METHODS

The *Ulmus* species used in these studies were selected at the University of Wisconsin experimental farms, Arlington, WI, and at the Morton Arboretum, Lisle, IL. These sources are indicated in the text by a *W* or *M* preceding the identification number. Relative susceptibility of these trees to *S. ulmea* had been determined previously in field surveys (12,13). Selected clones were propagated by leaf-bud cuttings or rooted from shoots taken from root cuttings. The latter method allowed for successive harvests of shoots from the same root section at 3- to 4-wk intervals. Unless otherwise noted, rooted cuttings and shoots were transplanted to Pro-mix (Premier Brands, New Rochelle, NY) in 6.35-cm-diameter

plastic pots and grown in a controlled environment chamber (24 ± 2 C, 12/12 or 8/16 photoperiod, ~375 μE/m^2/sec) for at least 3 wk prior to inoculation.

The inoculum in the following studies consisted of macroconidia (10^6 spores per milliliter) of *S. ulmea* which were atomized on plants until all the leaves were thoroughly wetted. Macroconidia were obtained by washing spores from lesions on leaves that had been inoculated in the growth chamber with conidia or ascospores 3 wk previously. Ascospores for inoculum increase were obtained from infected overwintered leaves, collected in early spring prior to spore release on the University of Wisconsin campus and at the University of Wisconsin's experimental farms at Arlington, WI. These were frozen until needed. When large numbers of ascospores were required, the overwintered leaves were soaked in water for 1 hr and passed between the two rubber rollers of a wringer mechanism from an old washing machine. The liquid expressed from the soaked leaves contained a dense suspension of ascospores that served as a source of initial inoculum.

Moisture. To determine the duration of moisture required for completion of the infection process, 16 individuals from each of two clones [(M559-64)-3 (M559-64)-11] derived from open-pollinated seed of *U. laevis* (M559-64) were incubated in a dew chamber (Percival Manufacturing Co., Boone, IA) at 16 C for various lengths of time (0–36 hr) after inoculation. Temperature adjustments (wall 10 C, pan 21 C) were such that moisture was maintained on the leaf surfaces at all times during incubation. Two individuals from each clone were removed at 0, 12, 24, and 36 hr after inoculation and were placed in a growth chamber at 16 C. Total number of lesions were counted 10 and 17 days after inoculation.

Temperature. Studies to determine the optimum temperature for symptom expression utilized the following individuals, selected in the field to provide a range of susceptibility to *S. ulmea*: *U. laciniata* W441-4, resistant (Koren introduction—probably containing *U. pumila* germ plasm); *U. laevis* (M1302-27)-1, susceptible (seedling of M1302-27); *U. pumila* W417-4, moderately susceptible; and *U. pumila* × *japonica* W44-11, resistant. Immediately following inoculation, plants were transferred to dew chambers set at 12, 16, 20, 24, or 28 C for 24 hr. They were then removed to growth chambers at the same temperatures. Two sets of four cuttings each per clone per temperature were evaluated for the number of plants per set exhibiting symptoms and type of lesion (sporulating or nonsporulating) 3 wk after inoculation. The experiment was repeated twice.

Several combinations of dew chamber and growth chamber temperatures were used to study the combined effects of incubation temperatures (the first 24 hr of the infection process) and latent period temperatures (2–3 wk following incubation) on subsequent disease frequency. Sixty rooted cuttings of *U. laevis* (M1302-27)-1 and 45 of *U. pumila*, W417-4, were divided into three equal groups and placed in dew chambers set at 12, 20, and 24 C immediately following inoculation. After 24 hr of dew treatment, the groups were further subdivided into sets of three or four plants each and placed in growth chambers maintained at 12, 16, 20, 24, or 28 C. This design allowed for every possible combination of the three dew chamber and the five growth chamber temperature regimes. Sets of plants were scored for the fraction infected and for the type of lesion (sporulating or nonsporulating) 3 wk after inoculation.

Leaf maturity. In previous studies, variation in the size and frequency of leaf spots on the leaves of an individual plant was noted. To determine whether leaf maturity was an important variable in the infection process, the length and nodal position of leaves on 16 cuttings each of *U. laevis* (M1302-27)-1 and *U. laciniata* W441-4 were recorded prior to inoculation. Nodal positions were numbered sequentially down the stem beginning with position 1 being the youngest and smallest leaf below the growing tip. The leaf in the bud, position 0, was not measured. Three weeks after inoculation, number and average size of lesions and length of the leaves was recorded. Analysis was based on the nodal position which reflects a leaf's maturity. At the time of inoculation, each plant had six to eight leaves on a single stem.

Repeatability estimates. The following six clones were used to estimate the repeatability of response to inoculation with *S. ulmea*: *U. laciniata* (W441-4); *U. pumila* × *U. pumila-rubra* (W418 × W425-1); *U. pumila* × *U. japonica* (W44-11); *U. pumila* (W417-4); *U. pumila* (W418); *U. laevis* [(M1302-27)-1]. Immediately after inoculation, plants were placed in an infection box instead of a dew chamber because of space limitations. The infection box consisted of a Plexiglas box 126 × 77 × 90 cm draped with cheesecloth and placed inside the growth chamber. Light intensity was reduced to ~ 150 μE/m^2/sec. A humidifier (9.5 L capacity) in the box was set to maintain 100% humidity for the first 24 hr and 80–100% humidity for the remainder of the latent period. The chamber was maintained at 16–20 C for the duration of the study. Three weeks after inoculation the number of plants exhibiting symptoms (fraction infected); the lesion type (no lesion = 0, nonsporulating = 1, sporulating = 2); and disease severity was recorded. The disease severity score was based on the most heavily infected leaf per plant and was scored according to the leaf index (Fig. 1) adapted from Trumbower (21) in which categories A through F were assigned respective scores of 0–5. The experiment was replicated three times with 16 rooted cuttings of each clone in a replicate. Repeatability

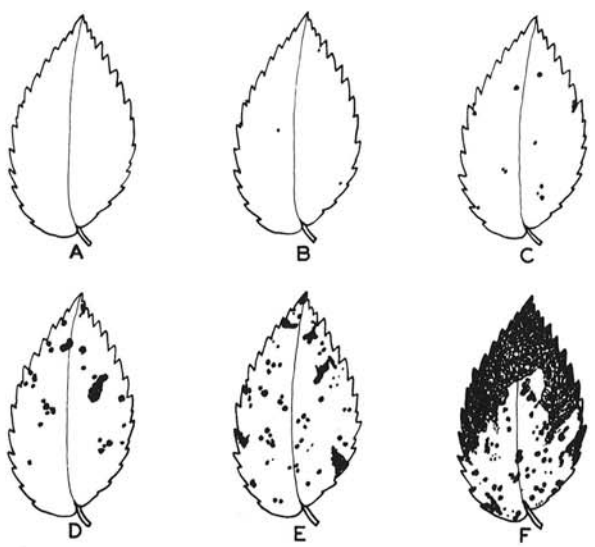

Fig. 1. Individual leaf disease assessment key used to evaluate the severity of black spot of elms. Each category was assigned a value as follows: A = 0, B = 1, C = 2, D = 3, E = 4, and F = 5.

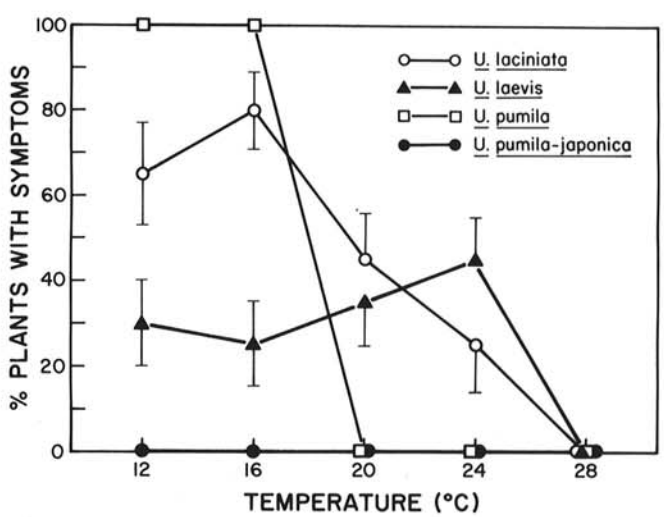

Fig. 2. The effect of temperature on black spot disease frequency in *Ulmus* spp. Each point represents mean percent of 16 rooted cuttings that exhibited foliar symptoms 3 wk after inoculation with macroconidia of *Stegophora ulmea*.

estimates (R) were computed from the components of variance as follows (1,6):

$$R = \sigma_w^2/(\sigma_w^2 + \sigma_e^2)$$

in which σ_w^2 = [(clone mean square)−(error mean square)]/(total measurements per clone) and σ_e^2 = error mean square.

RESULTS

Moisture. Exposure to moist periods of various duration resulted in highly significant differences ($P = <0.01$) in lesion frequency in the more susceptible clone [(M559-64)-11] after 17 days. Counts made on day 10 did not exhibit significant differences. The greatest number of lesions (mean lesions per plant = 235 ± 38) were recorded for plants that had been incubated in the dew chamber for 24 hr; significantly fewer lesions were found on plants that had been incubated for 12 and 36 hr (mean lesions per plant = 32 ± 14 and 54 ± 6, respectively). No lesions were produced on plants that were not exposed to dew periods. The results were similar (no lesions after 0 and 36 hr of exposure), but differences among exposure periods were not significant for the less susceptible clone [(M559-64)-3] due to within-clone variation.

Temperature. Temperature significantly affected the fraction of infected plants in clones of *U. laciniata* and *U. pumila* (Fig. 2). Temperature did not have a significant effect on the cloned plants of the hybrid *U. pumila* × *japonica*, which exhibited no symptoms at any temperature or on the cloned plants of *U. laevis* in which similar fractions were infected at all temperatures except 28 C. Lesion type was not influenced by temperature; *U. laciniata* and *U. pumila* consistently developed nonsporulating lesions and *U. laevis* produced typical sporulating lesions at all temperatures except 28 C.

When dew chamber and growth chamber temperatures were varied factorially, the growth chamber temperature caused a significant variation in fraction of plants infected (Table 1). Insufficient replication precluded analysis of the effect of dew chamber temperature. Again, low temperatures favored symptom expression in *U. pumila*, and a broader range was acceptable in *U. laevis*. Chlorotic flecks, which were not counted as lesions, were present on *U. laevis* at 28 C in this study.

Leaf maturity. The initial average length of leaves measured in this study ranged from 9 mm (position 1) to 66 mm (position 4) in the *U. laevis* clone and from 7 mm (position 1) to 62 mm (position 5) in the *U. laciniata* clone. Leaves that were <10 mm long were always closed, ie, folded at the midrib. Leaves measuring between 13 mm and 26 mm were half open and leaves over 30 mm long were usually fully opened in both clones. The relationship between nodal position and leaf elongation over the 3-wk period is illustrated in Fig. 3. From this graph it is clear that rapid elongation and subsequent expansion occurred in leaves in nodal positions 1, 2, and 3. Leaves in positions 4, 5, and 6 had ceased rapid growth and were close to their maximum length.

For both clones, leaf position (and therefore leaf maturity) was a highly significant factor in determining the number of lesions. The maximum number of lesions was recorded for leaves that were in position 2 at the time of inoculation (Fig. 4). No lesions were recorded for leaves in nodal positions 4, 5, or 6. Since these were the largest leaves at the time of inoculation, the amount of exposed leaf tissue is not a factor in leaf susceptibility. Leaves in position 2 were also the most rapidly elongating (Fig. 3). A good correlation (r = 0.67) between lesion number and leaf elongation suggests increased susceptibility in rapidly growing leaves.

The relationship between lesion diameter and leaf position was also highly significant ($P = <0.01$) (Fig. 5). The largest lesions were found on leaves in position 1, which were the smallest measured leaves at the time of inoculation. The negative correlation between lesion size and leaf size, $r = -0.54$ (*U. laevis*) and $r = -0.43$ (*U. laciniata*), confirms this.

Repeatability estimates. Clone mean scores for each assessment method are presented in Table 2. The repeatability estimates obtained from the variance components ranged between 0.910 ± 0.003 for assessment by fraction infected and 0.889 ± 0.068 for assessment by lesion type to 0.878 ± 0.072 for assessment according to individual leaf disease severity. These estimates were based on standard methods of repeatability analysis (1,6) in which the total observed phenotypic variance is partitioned into the within-clone variance (error) and the between-clone variance. The repeatability of a character is the ratio of the between-clone variance to the total phenotypic variance. When the block × clone interaction was included, the values were reduced and ranged between 0.728 and 0.600.

DISCUSSION

The results of this study have been applied to the development of a standardized screening procedure. The need for expanding leaves indicates that the preinoculation environment is also an important variable. Since elms enter dormancy when grown at low temperatures under a 12/12 light/dark regime, plants to be screened should be grown at ~24 C for at least 3 wk prior to inoculation to stimulate vigorous growth. After inoculation, 24 hr of dew treatment is recommended, followed by incubation at low temperatures (12–16 C) for 3 wk prior to evaluation.

TABLE 1. Effect of temperature during incubation and latent periods on fraction of plants of *Ulmus* species exhibiting symptoms caused by *Stegophora ulmea*

Ulmus spp. clones and dew-chamber[a] temperatures (C)	Growth chamber temperature (C)				
	12	16	20	24	28
U. laevis M1302-27-1					
12	4/4[b]	4/4	4/4	4/4	0/4
20	1/3	4/4	4/4	4/4	0/4
28	0/4	2/4	4/4	1/4	0/4
U. pumila W417-4					
12	3/3	3/3	0/3	0/3	0/3
20	2/3	3/3	0/3	0/3	0/3
28	2/2	1/3	0/3	0/3	0/3

[a] Dew chambers were adjusted so that a thin film of water was maintained on the leaf surfaces during the incubation period (24 hr). After incubation plants were transferred to growth chambers until symptoms were evident (latent period).

[b] Fraction of plants with symptoms 3 wk after inoculation with macroconidia of *S. ulmea*.

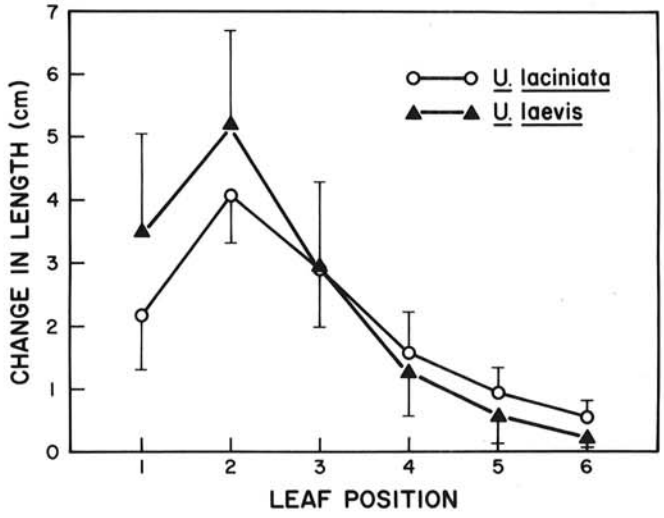

Fig. 3. Elongation of leaves of *Ulmus* spp. in relation to their maturity as determined by leaf (nodal) position. Positions were numbered sequentially with position 1 at the growing tip. Each point represents the mean change in length in 16 leaves over a 3-wk period.

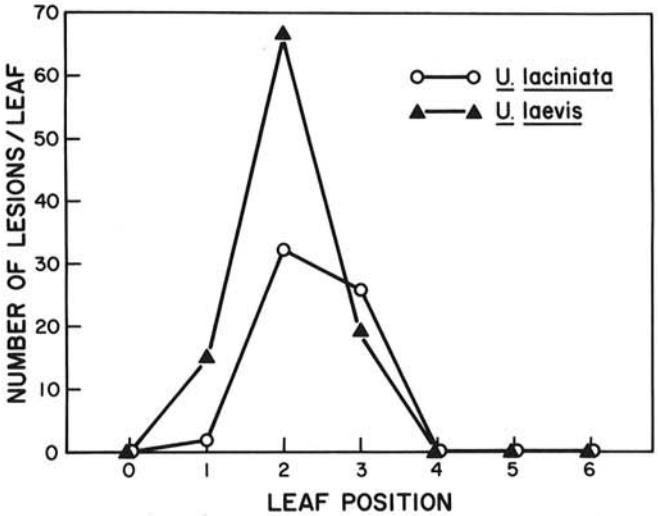

Fig. 4. The relationship between *Ulmus* spp. leaf maturity, as determined by (nodal) position, and the frequency of lesions caused by *Stegophora ulmea*. Positions were numbered sequentially down the stem. Position 0 was a bud at time of inoculation. Each point represents the mean number of lesions per leaf on 16 leaves 3 wk after inoculation with macroconidia (pooled SD = 26.4).

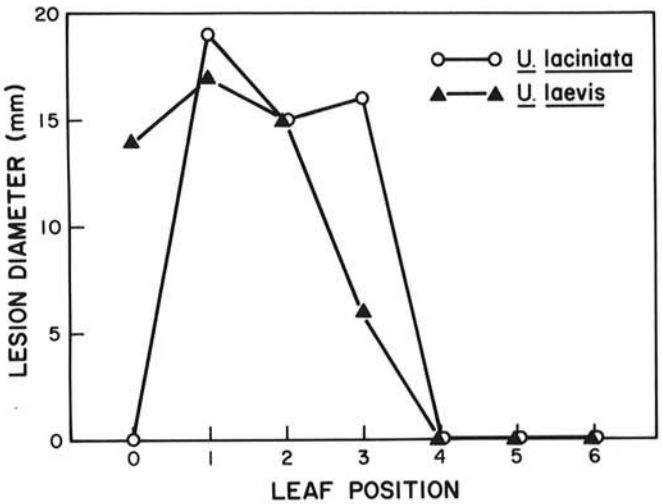

Fig. 5. Relationship between leaf maturity of *Ulmus* spp. as determined by (nodal) position, and diameters of lesions caused by *Stegophora ulmea*. Positions were numbered sequentially down the stem. Position 0 was a bud at time of inoculation. Each point represents the mean lesion diameter on 16 leaves 3 wk after inoculation with macroconidia (pooled SD = 0.09).

The temperature studies suggest that the resistance of the *U. laciniata* and the moderate susceptibility of the clone of *U. pumila* in the field may be due to the narrow temperature range favorable for infection as well as the lack of a source of secondary inoculum on these hosts which generally produce nonsporulating lesions. *U. laevis*, which is highly susceptible in the field, exhibited symptoms over a broad temperature range and consistently developed sporulating lesions. Whether higher temperatures could be used to separate the moderately from the highly susceptible hosts requires further examination.

Our results indicate that leaves go through a period of susceptibility which is greatest immediately after the leaves open and decreases rapidly thereafter. A maximum of three leaves was susceptible at one time—these were young, expanding, and near the bud. The susceptibility of closed leaves (position 1) may not have been adequately tested in this study if their adaxial surfaces were not exposed uniformly to the inoculum. Our data on the resistance of mature leaves contradict the results of Pomerleau (16) in which he found an increasing frequency of leaf spots in the field through September. Field observations in Wisconsin suggest that leaf spot frequency increased rapidly under favorable environmental conditions until July, after which new lesions are found only on trees that continue to send out new shoots. The necrotic area around lesions on mature leaves does enlarge and become more conspicuous later in the season.

Several methods were used to evaluate the susceptibility of the host plants. These include lesion counts, lesion types (sporulating and nonsporulating), fraction of plants infected, and disease severity based on the leaf index scale of severity. In the final study, which was designed to estimate the repeatability of the host response, the latter three methods were compared. Assessment according to fraction of plants infected and individual leaf disease severity did not separate the clone of *U. laciniata* (resistant in field studies) from the clone of *U. laevis* (highly susceptible in field studies). The results determined by lesion type evaluation were more representative of the reaction of these clones in the field.

All three methods of evaluation resulted in high repeatability estimates (0.88–0.91). Houston and Stairs (9) obtained estimates of 0.511 to 0.818 in growth-chamber screening for air pollution tolerance in eastern white pine (*Pinus strobus* L.) and concluded that the response was under strong genetic control. Karnosky (10), also working with air pollution tolerance under controlled conditions, reported that repeatability estimates of 0.464–0.642 suggested that tolerance was under strong genetic control in trembling aspen (*Populus tremuloides* Michx.). Hansche and Brooks (7) concluded that substantial improvement could be made in specific characters of sweet cherry (*Prunus avium* L.) that had heritabilities (repeatabilities) of 0.22–0.87.

TABLE 2. Mean disease scores for clonal response to inoculation with *Stegophora ulmea* based on three methods of disease assessment

Clone	Mean disease score[w]		
	Fraction infected[x]	Severity[y]	Lesion type[z]
U. pumila × *japonica* W44-11	0.000 a	0.000 a	0.000 a
U. pumila W417-4	0.021 a	0.021 a	0.021 a
U. pumila (*U. pumila* × *rubra*) W418 × W425	0.076 a	0.77 ab	0.77 a
U. pumila W418	0.583 b	1.031 bc	0.910 b
U. laciniata W441-4	0.783 bc	1.367 c	1.047 c
U. laevis M1302-27-1	0.861 c	1.855 c	1.685 d

[w] Sixteen rooted cuttings from six sources were tested. Inoculum suspension containing 10^6 macroconidia per milliliter was atomized on plants 3 wk before disease assessment. The experiment was replicated three times. Means followed by the same letter in a column do not differ significantly at $P = 0.05$ (Duncan's multiple range test).

[x] Fraction infected was based on the fraction of plants exhibiting foliar symptoms.

[y] Disease severity was based on an individual leaf disease assessment key. The most severely infected leaf of each plant was rated on a scale ranging from 0 (no disease) to 5 (at least 75% necrosis).

[z] Lesion types were recorded numerically as 2 = sporulating, 1 = nonsporulating, and 0 = no lesions.

Repeatability estimates are considered to be the upper limit of both the heritability of a trait and a measure of the genetic determination of a character (6). A high heritability estimate suggests that selection on the basis of phenotype will be successful, especially if selection is undertaken in a controlled environment that reduces the environmental variance. Because the individuals in this study were selected in the field for their relative degree of susceptibility, it also appears that field selection in areas where black spot is abundant also will be successful.

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