

Resistance

Development of Rust on Asparagus Cultivars After Inoculation with Basidiospores, Aeciospores, and Urediniospores of *Puccinia asparagi*

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ABSTRACT

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Asparagus cultivars were inoculated with urediniospores and aeciospores in the greenhouse and with basidiospores in the greenhouse and in the field. Latent period and numbers of pustules were determined. Number of aecia per shoot varied significantly ($P = 0.05$) among cultivars after infection by basidiospores. Latent period and number of uredinia per linear centimeter of shoot varied significantly ($P = 0.05$) among cultivars after infection by either aeciospores or urediniospores. Length of latent period and number of uredinia after either urediniospore or aeciospore infection in the greenhouse were correlated with the area under the disease progress curve (AUDPC) measured in the field. However, latent period and number of uredinia of some individual cultivars with low values of AUDPC did not differ significantly ($P = 0.05$) from those of cultivars with high AUDPC values. Therefore, monocyclic test

measurements of components of rust resistance in the greenhouse should not be used to supplant field epidemics when selecting for resistance in asparagus. Number of aecia was not correlated with severity of rust in the field or with latent period or number of uredinia after either aeciospore or urediniospore infection. Latent period after aeciospore infection in the greenhouse was positively correlated with latent period ($P = 0.01$) after urediniospore infection and negatively correlated with number of uredinia ($P = 0.05$) after urediniospore infection. Thus, cultivars reacted similarly when infected with either aeciospores or urediniospores, and they reacted differently in three of 12 cultivars when infected with either urediniospores or basidiospores. Mature asparagus shoots were resistant to infection by basidiospores.

Puccinia asparagi DC. is an autoecious, macrocyclic rust of asparagus (*Asparagus officinalis* L.). Severe rust epidemics occur sporadically in south central Washington, where more than 12,000

ha of asparagus are grown. Pycnia, aecia, uredinia, and telia of *P. asparagi* can be observed during most years and are important in the development of rust epidemics (10). The fungus overwinters as teliospores on infested asparagus debris. Pycnia and then aecia occur in the same lesion on volunteer asparagus and on shoots

not harvested in the spring. Aecia are an early source of inoculum; they are eliminated when shoots are harvested. If all shoots were harvested, epidemics would not develop further (10,11). Uredinia appear on foliage after the spring cutting period, and severe infection reduces yield the following cutting season (11).

The quantitative type of resistance, the only type of rust resistance reported in the genus *Asparagus* (2,6,8,10,16), is practical for management of asparagus rust (10). More detailed information on quantitative resistance in asparagus should improve disease management. Asparagus cultivars show differential responses in production of aecia and uredinia (3,8,11). This study investigated length of latent period and number of pustules after monocyclic infection by urediniospores, basidiospores, and aeciospores of *P. asparagi* on asparagus cultivars that had low and high values of the area under the disease progress curve (AUDPC) when infected with urediniospores in the field. Such information may increase understanding of the nature of rust resistance in asparagus and aid in developing rust-resistant asparagus cultivars.

MATERIALS AND METHODS

Twelve asparagus cultivars were studied. Seed of WSU-1, WSU-2, Wash T2, and Delmonte 361 was obtained from the Washington Asparagus Growers Association, Sunnyside, WA; seed of Mary Washington was produced by Glen Smith, Sunnyside, WA; seed of Jersey Giant, Jersey Centennial, 277C × 22-8, and D2 × 22-8 came from J. H. Ellison, Rutgers University, New Brunswick, NJ; and UC 157, UC 72, and UC-Ida Lea came from the University of California, Riverside. Seed was germinated in darkness on moistened filter paper in petri dishes at 25 C. Thirty germinated seeds per cultivar were planted in a silt loam soil from virgin sagebrush land with one plant per pot (16 cm in diameter) in a greenhouse. Asparagus does not have a physiological dormancy; it grows continuously in a warm greenhouse. Plants were fertilized with 0.15 g of 34-0-0 NH₄NO₃ each month for 12 mo. Foliage was then removed to release apical dominance, which stimulated new shoot emergence. From the population of 30 plants per cultivar, new stems of eight plants of each cultivar in a similar growth stage were selected for inoculation.

Urediniospore inoculation. Urediniospores were originally collected from an asparagus field north of Pasco, WA; increased from a single uredium on WSU-1 in the greenhouse; and collected the day of inoculation. Primary shoots (main stem) in the 50–75% cladophyll stage of development (6) of each cultivar were inoculated with urediniospores of *P. asparagi* in a randomized

complete block design with eight replications in 1987 and five replications in 1989. Tests were not done in 1988 in the greenhouse. Two cultivars were not included in the 1989 test because seed was not available from the original source (Table 1). A 35-cm, central section of each shoot was atomized with 0.3 ml of an oil suspension (Soltrol 170) of 1.1×10^6 urediniospores per milliliter from a size 00 gelatin capsule using a spore-oil suspension atomizer (4) at an air pressure of 60 kPa. After the oil evaporated, plants were placed in a mist chamber at 20–23 C for 24 hr and then returned to the greenhouse. Natural light supplemented with fluorescent lamps providing about 18 W/m² was used to provide a photoperiod of 15 hr/day. Temperatures ranged from 21 to 26 C during the day and from 17 to 20 C at night.

Uredinia from initial points of infection (10) were counted on primary shoots every day after inoculation for 10 days and then on alternate days for six more days. Latent period was calculated by regression analysis of probit percent of uredinia on days after inoculation (14). The number of uredinia per linear centimeter of shoot length was determined from the total number of uredinia on a primary shoot divided by 35 cm.

Basidiospore inoculations. In March 1987, foliage of 18-month-old crowns was removed except for one shoot per crown that was near the 100% cladophyll stage of development (6). After new shoots had emerged and before cladophylls were visible, 10 g of asparagus debris bearing telia was placed in pots of each cultivar that were arranged in a randomized complete block of eight replicates. Asparagus debris had been collected the previous fall from field plots where plants were severely rusted, and had been stored outside for the winter. Twenty-four hours before inoculation, stems and branches with telia were taken from the debris, cut to about 10-cm lengths, tied in 10-g bundles, and soaked in water at 16 C (1). Pots with plants and debris were placed in a mist chamber at 16–18 C for 49 hr and then moved to a greenhouse at 21–26 C during the day and 17–21 C at night. Pycnia appeared 7 days after plants were placed in the mist chamber, and then aecia formed in the same lesions. Pycnia and aecia were counted daily until 14 days after inoculation. Latent period was not estimated because plants were kept in the mist chamber longer than 24 hr. The number of aecia per stem was counted on both young and mature shoots.

Single-row plots containing 10 plants of each cultivar, in a randomized complete block design of four replicated, were established with transplants onto a fine sandy loam soil at the Irrigated Agriculture Research and Extension Center near Prosser, WA, in April 1986. Transplants were spaced 30 cm apart,

TABLE 1. Area under the disease progress curve (AUDPC), latent period and infection frequency of asparagus cultivars infected with basidiospores, aeciospores, or urediniospores of *Puccinia asparagi*^a

Cultivar	AUDPC ^c			Urediniospore infection				Aeciospore infection ^b		Basidiospore infection (Aecia/stem)		
				Latent period (days)		Uredinial linear cm		Latent period (days)	Uredinia/linear cm	Greenhouse ^b	Field ^c	
	1987	1988	Mean	1987 ^b	1989 ^d	1987 ^b	1989 ^d				1987	1989
WSU-1	1998 a	2179 a	2089 a	7.7 a	7.7 a	0.4 bc	1.5 a	9.6 abc	0.06 abc	79 a	8.3 a	5.5 ab
WSU-2	1032 bc	1698 b	1365 b	7.7 a	8.1 abc	1.1 ab	1.3 ab	8.9 a	0.07 ab	20 b	4.9 ab	4.0 abc
UC-72	1103 b	1588 b	1346 b	7.7 a	8.0 ab	1.5 a	0.6 bc	9.4 ab	0.03 bcd	54 ab	1.0 bc	5.6 ab
Wash-T2	1028 bc	1500 bc	1264 b	8.0 ab	8.5 abc	0.3 c	0.5 bc	9.4 ab	0.08 a	36 ab	2.5 abc	3.6 abcd
M. Washington	790 c	1269 c	1030 c	8.3 abc	7.9 ab	0.4 bc	1.2 ab	10.0 abcd	0.03 bcd	17 b	0.6 c	2.3 bcd
UC-157	236 d	683 d	460 d	9.0 cd	8.9 cd	0.1 c	0.2 c	10.0 abcd	0.02 cd	45 ab	8.6 a	10.5 a
UC-Ida Lea	170 d	681 d	426 de	8.7 bcd	...	0.2 c	...	9.7 abc	0.03 bcd	15 b	0.3 c	2.4 bcd
Jersey Giant	287 d	494 de	391 de	9.6 d	9.9 e	0.1 c	0.1 c	11.5 de	0.01 d	9 b	0.8 c	1.8 cd
Delmonte 361	156 d	614 de	385 de	8.7 bcd	9.6 de	0.1 c	0.2 c	11.6 e	0.01 d	12 b	1.1 bc	3.6 abcd
D2 × 22-8	246 d	422 de	334 de	8.7 bcd	...	0.1 c	...	10.6 bcde	0.02 cd	21 ab	2.4 abc	1.4 d
J. Centennial	147 d	407 de	277 de	8.8 bcd	8.9 cd	0.2 c	0.1 c	11.0 cde	0.01 d	21 ab	2.1 abc	1.9 cd
277C × 22-8	96 d	335 e	216 e	8.7 bcd	8.8 bcd	0.2 c	0.1 c	11.3 de	0.01 d	68 a	1.5 abc	7.4 a

^aWithin a column, values with same letter are not significantly different at $P = 0.05$ according to Duncan's multiple range test.

^bValues are means of eight replicates.

^cValues are means of four replicates.

^dValues are means of five replicates.

rows were 1.5 m apart, and the plot area was surrounded by a border of WSU-1. In April 1987 and April 1989, 5- and 10-g bundles, respectively, of asparagus debris with telia were soaked in 16 C water for 24 hr, and a bundle was placed near emerging shoots at two locations, separated by at least 50 cm, in each plot. Asparagus debris from the previous season was hand raked from nearby plots before shoot emergence in 1989. Plots were sprinkler-irrigated the night of inoculation for 9 hr in 1987 and 12 hr in 1989. Debris used for an inoculum source was removed the next day. Aecia were counted on shoots 18 and 22 days after inoculation in 1987. In 1989, temperatures were lower, and aecia were counted 23 and 27 days after inoculation.

Aeciospore inoculation. In April 1987, foliage was removed from 19-mo-old crowns in the greenhouse to stimulate new shoot emergence. New primary shoots of cultivars in the 50–75% cladophyll stage of development were inoculated with 0.3 ml of an oil suspension of aeciospores. The experiment was a randomized complete block with eight replications. A 35-cm section of the primary shoot was atomized as when inoculated with urediniospores. Shoots with aecia were cut from the field the previous day, placed in a 1,000-ml beaker with 400 ml of distilled water, and covered with a polyethylene bag overnight; aeciospores were then collected from aecia. Because of the limited number of aeciospores collected per day, each replication was inoculated on a separate day. Five replicates were inoculated with 1×10^6 and three with 2×10^5 aeciospores per milliliter. After inoculation, plants were placed in a mist chamber for 24 hr and then in the greenhouse at 21–27 C during the day and 17–21 C at night. Lighting, photoperiod, number of days uredia were counted, calculation of latent period, and number of uredia per linear centimeter of stem were the same as for plants inoculated with urediniospores. Uredinia were counted only on the main stem unless none developed there; then they were counted on branches and cladophylls for determination of latent period. Lengths of latent period on the main stem, branches, and cladophylls were similar within a cultivar (Johnson, unpublished). Uredinia per linear centimeter of shoot were calculated only for the main stem.

Development of uredinia in the field. In 1987 and 1988, field plots were sprinkler-irrigated at night for 8–12 hr at 10- to 14-day intervals to induce uredinia to develop. Rust severity was estimated as the proportion of surface area of the foliage of each plot covered with uredinia by using the modified Cobb's scale for cereal stem rust (12). Rust severity was estimated six times at 14-day intervals beginning 7 July in 1987, and five times at 14-day intervals beginning 27 July in 1988. The AUDPC was calculated for each plot.

Data were analyzed with analysis of variance, and means were compared using Duncan's new multiple range test. Number of uredinia per linear centimeter after inoculation with

urediniospores and number of aecia per stem were transformed to $\log(1 + X)$ to reduce the heterogeneity of the variances of the treatment means (15). Linear correlation was used to determine the relationship of the various components of disease development with each other and with AUDPC. When experiments were repeated, a mean for each cultivar from the two experiments was used in the correlation analysis.

RESULTS

Severe rust epidemics developed on plants in the field in 1987 and 1988. Disease severity of some plots reached 90% in 1987 and 80% in 1988. During both years, AUDPC varied significantly ($P = 0.05$) among the 12 cultivars (Table 1), and AUDPC was significantly correlated ($P = 0.01$) for the 12 cultivars. Correlation coefficient was 0.97. Rust development was most severe ($P = 0.05$) on WSU-1, followed by UC-72, WSU-2, Wash T2, and then Mary Washington. The other seven cultivars (UC-157, UC-Ida Lea, Jersey Giant, Delmonte 361, D2 \times 22-8, Jersey Centennial, and 277C \times 22-8) had significantly lower ($P = 0.05$) AUDPC values (Table 1).

Number of aecia per stem, latent period, and number of uredinia per linear centimeter of shoot varied significantly ($P = 0.05$) among cultivars when infection resulted from inoculation with basidiospores, aeciospores, or urediniospores (Table 1). The cultivars Jersey Giant and UC-157 in 1987 and Jersey Giant, UC-157, Delmonte 361, and Jersey Centennial in 1989 had significantly ($P = 0.05$) longer latent periods after infection by urediniospores than did cultivars WSU-1, WSU-2, UC-72, Wash-T2, and Mary Washington (Table 1). The cultivars Jersey Giant, Delmonte 361, and 277C \times 22-8 had significantly ($P = 0.05$) longer latent periods after infection by aeciospores than did cultivars WSU-1, WSU-2, UC-72, Wash-T2, and Mary Washington (Table 1). Many components of disease development of individual cultivars with low values of AUDPC did not differ significantly from those of cultivars with high values of AUDPC. For example, latent period after urediniospore infection of 277C \times 22-8, Jersey Centennial, D2 \times 22-8, Delmonte 361, and UC-Ida Lea did not differ significantly ($P = 0.05$) from that of Wash-T2 and Mary Washington in 1987 (Table 1).

Latent period after aeciospore infection was positively correlated with mean latent period after urediniospore infection ($P = 0.01$) and mean AUDPC ($P = 0.01$), and it was negatively correlated with mean uredinia per linear centimeter ($P = 0.01$) after urediniospore infection (Table 2). Mean latent period after urediniospore infection was negatively related to mean uredinia per linear centimeter ($P = 0.01$) after urediniospore infection and to AUDPC ($P = 0.01$) in the field (Table 2).

Numbers of aecia per stem were not correlated with value of AUDPC of the cultivars (Table 1). UC-157 and 277C \times 22-8

TABLE 2. Correlation coefficients for relationships between area under the disease progress curve (AUDPC) and two components of disease development and among the components of disease development of asparagus cultivars infected with basidiospores, aeciospores, or urediniospores of *Puccinia asparagi*

	Basidiospore infection (aecia/stem)		Aeciospore infection		Urediniospore infection		Mean AUDPC
	Greenhouse	Field	Latent period	Uredinia/ linear cm	Latent period	Uredinia/ linear cm	
Basidiospore infection							
Greenhouse	1.00	0.66 ^a	-0.24	0.23	-0.45	0.23	0.48
Field	...	1.00	-0.30	0.22	-0.23	0.18	0.31
Aeciospore infection							
Latent period	1.00	-0.82 ^b	0.82 ^{**}	-0.75 [*]	-0.74 ^{**}
Uredinia/linear cm	1.00	-0.71 ^{**}	0.66 [*]	0.80 ^{**}
Urediniospore infection							
Latent period	1.00	-0.86 ^{**}	-0.83 ^{**}
Uredinia/linear cm	1.00	0.88 ^{**}
AUDPC	1.00

^a * Indicates correlation coefficient significant at $P = 0.05$.

^b** Indicates correlation coefficient significant at $P = 0.01$.

had low AUDPC values, few uredinia per linear centimeter of shoot, and relatively long latent periods when infected with urediniospores and aeciospores, but they were relatively susceptible to infection by basidiospores (Table 1). Mary Washington was susceptible to infection by urediniospores and relatively resistant to infection by basidiospores. WSU-1 was susceptible and Jersey Giant was resistant to the three types of infecting spores. Number of aecia on shoots was not significantly correlated to latent period or number of uredinia per linear centimeter after either aeciospore or urediniospore inoculations (Table 2). In the greenhouse, means of 9–79 aecia developed on the young, elongating shoots of the cultivars (Table 1), and none developed on the mature shoots. The difference was statistically significant ($P = 0.01$).

Data from the two inoculation experiments with basidiospores in the field were significantly correlated ($P = 0.05$). The correlation coefficient was 0.63. The mean number of aecia per stem for cultivars from the two experiments in the field were significantly correlated ($P = 0.05$) with the number of aecia per stem from the inoculation with basidiospores in the greenhouse (Table 2).

DISCUSSION

Not all cultivars in this study with low AUDPC values differed significantly from cultivars with high AUDPC values in length of latent period and number of uredinia. This suggests several possibilities. First, components of rust resistance in asparagus, in addition to latent period and number of uredinia, may have an important effect on disease development in the field. Second, even though some values were not significantly different, values for the latent period were larger and values for the number of uredinia were smaller for cultivars with low AUDPC values than they were for cultivars with high AUDPC values. Such differences, over a long season of many infection cycles, may have an important effect on disease development in the field. Third, controlled environments in a greenhouse or growth chamber differ from the environment in the field, which affects research results. For example, the difference in mean latent period between rust-resistant and rust-susceptible wheat cultivars of *Triticum aestivum* L., infected with *P. recondita* Rob. ex Desmaz. f. sp. *tritici* (Erikss.) C.O. Johnston, was 1.8–4 times greater in the field than when measured in growth chambers (7). Fourth, a cultivar may contain one component of resistance and not another. For example, some wheat cultivars contain two types or components of resistance to scab, caused by *Fusarium roseum* (Link) emend. Snyder & Hans. f. sp. *cerealis* (Cke. Snyder & Hans.), which are resistance to initial infection and resistance to the spread of the fungus within a plant, whereas other cultivars only contain one or the other of these components (13).

Therefore, the important message from this study is that monocyclic test measurements of components of rust resistance in controlled environments do not adequately evaluate field resistance of asparagus cultivars to rust. None of the greenhouse measures proved to be completely reliable and cannot be used to supplant field epidemics. Differences among cultivars were detected in the field using AUDPC, and this statistic would be a reliable selection criterion for resistance to urediniospore infection in asparagus (9).

Resistance in asparagus to urediniospore infection is paramount because of the infection's repeating cycle during a season environmentally favorable for rust development. Basidiospore infection and the subsequent development of aecia on asparagus is important for the buildup of inoculum of ensuing epidemics. Eliminating aecia on asparagus averts epidemic development (10,11). Reducing the number of aecia from basidiospore infection reduces inoculum during the early phases of an epidemic. In this study, susceptibility to basidiospore infection by itself did not appear to adversely affect the level of rust later in the season. For example, UC-157 was susceptible to infection by basidiospores and resistant to infection by both urediniospores and aeciospores, whereas Jersey Giant was resistant to infection by all three types of infecting spores. However, no significant difference was found

in AUDPC values between the two cultivars. Breeders should place emphasis on selecting for resistance to urediniospore infection. It is not possible, from data collected in this study, to completely quantify the effect of resistance to basidiospore and aeciospore infection on epidemic development, because aeciospore and urediniospore inoculum infected plants in adjacent plots.

Asparagus genotypes relatively resistant to urediniospore infection and susceptible to basidiospore infection have been noted previously (3,8,11) and also in this study. Cultivars responded similarly when infected with either aeciospores or urediniospores. A similarity of aeciospores and urediniospores is that both are dikaryotic and both differ from basidiospores, which are haploid. It appears that host resistance in asparagus to *P. asparagi* may depend on the nuclear condition (dikaryotic vs. haploid) of the infecting spore. H. H. Flor demonstrated that the host range of basidiospores differed from that of the aeciospores and urediniospores of the autoecious rust *Melampsora lini* (Ehrens.) Desmaz. (5). This phenomenon is certainly not identical to but does resemble infection by heteroecious rusts, in which haploid spores of the same rust species infect a different host than the dikaryotic spores. Flor suggested that this may be an intermediate step in the evolution of heteroecism (5).

Asparagus shoots that developed beyond the 100% cladophyll stage of development in the greenhouse were completely resistant to infection by basidiospores. In the field, I have observed newly formed pycnia and aecia only on young shoots; young, expanding secondary and tertiary branches; and young cladophylls. Asparagus shoots also become more resistant to infection by urediniospores as they mature (6,8).

The results of this study were similar to those of other studies (3,8). WSU-1, WSU-2, Wash T2, and Mary Washington were susceptible to and Jersey Giant (formerly, 56 × 22-8), UC-157, Delmonte 361, and Jersey Centennial were resistant to urediniospore infections. In Minnesota (3), WSU-1 and Wash T2 were susceptible to urediniospore infection and Jersey Centennial was resistant. Relatively few aecia per stem developed in the field on Delmonte 361, Jersey Giant, Jersey Centennial, and Mary Washington in this and a previous study in Washington (8) and on Jersey Centennial in Minnesota (3). WSU-1 and Wash T2 were very susceptible to basidiospore infection in this study and in the previous study in Washington (8), and WSU-1 was susceptible in Minnesota; Wash T2 was not significantly different either from WSU-1 or from the most resistant entry in the Minnesota study (3).

The number of uredinia per linear centimeter on WSU-1 after urediniospore infection was considerably lower in 1987 than in 1989 (Table 1). Values both years were greater, although not significantly greater in 1987, than those on all the slow-rusting cultivars. The larger value in 1989 was more typical of those observed in other inoculation experiments using WSU-1 (8,9). Variation in inoculation technique of asparagus with urediniospores (6) and the other spore types of *P. asparagi* may produce relatively large differences in numbers of pustules. Consistent and uniform application of inoculum is essential for successful experiments when observing numbers of pustules on asparagus.

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