Rust Resistance in Asparagus F_1 Hybrid Populations

DENNIS A. JOHNSON, Plant Pathologist, Washington State University, and RICHARD N. PEADEN, Research Agronomist, U.S. Department of Agriculture-ARS, Irrigated Agriculture Research and Extension Center, Prosser, WA 99350

ABSTRACT

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Rust severity was evaluated 3 yr in the field using the area under the disease progress curve (AUDPC) to classify rust resistance in 10 asparagus F_1 hybrid populations derived from crosses among parents resistant, moderately resistant, and susceptible to *Puccinia asparagi.* The effect of genotype on rust severity was highly significant, and progeny were continuously distributed from low to high AUDPC in all 10 populations, indicating quantitative inheritance. The estimate of heritability using regression of offspring on the male parent was 55%. Highly resistant parents from the cultivars Jersey Giant and Jersey Titan had significantly greater specific combining abilities than parents from moderately resistant or susceptible cultivars. Progeny means were significantly skewed toward low AUDPC values, suggesting dominant resistance. Transgressive segregation for resistance was not observed in populations from highly resistant parents, but it was observed in some populations from moderately resistant parents.

Puccinia asparagi DC. in Lam. & DC. is an autoecious, macrocyclic rust that occurs sporadically in south central Washington, where more than 11,500 ha of asparagus (*Asparagus officinalis* L.) are grown. Rust epidemics are associated with rain or frequent dews (14). Yields of susceptible asparagus cultivars were substantially reduced by rust epidemics, whereas yields of resistant cultivars were not (12).

Resistance to rust in asparagus is recognized as an efficient means of managing rust (4,8). Since the early 1900s, much effort has been directed toward identifying and developing resistant asparagus cultivars (3,8–10,16). Rust resistance used in asparagus cultivars has been quantitative rather than qualitative, resulting in differences in intensity of infection (2,8,9,16,19). In a greenhouse study, seedling progeny derived from resistant or susceptible cultivars consistently performed similarly to their parents (8). However, estimates of heritability for rust resistance, using number of pustules per plant as the statistic indicating resistance, were less than 20% (8).

Variation for rust resistance has been found within the rust resistant cultivars Jersey Giant, Delmonte 361, and Jersey Centennial, and the susceptible cultivars Mary Washington and WSU-1 (10). This was expected because asparagus cultivars consist of heterogeneous populations. Asparagus is dioecious, and cultivars grown in the United States are mostly either open-pollinated or clonal hybrids from heterozygous parents.

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Strains of cultivar Mary Washington were the most resistant selections used in a study on the inheritance of rust resistance reported in 1957 (8). Integrity for rust resistance of open-pollinated Mary Washington was not maintained because growers used seed from random pollination for new plantings (5,8,16). In a recent study, rust developed more slowly on the new asparagus cultivars Jersey Giant, Jersey Centennial, Delmonte 361, Jersey Titan, and UC-157 than on Mary Washington in Washington state (9). New cultivars Jersey Giant, Jersey Titan, and Jersey Centennial have higher levels of rust resistance than current selections of Mary Washington (3,5,6, 7,9). Little is known about the heritability of rust resistance from these newly developed rust resistant cultivars.

The purpose of this study was to field evaluate rust severity at the adult-plant stage of growth in 10 F_1 hybrid populations derived from parents with relatively high, moderate, and low levels of resistance to rust.

MATERIALS AND METHODS

Parents for crosses were selected during rust epidemics in 1983 and 1984 near Prosser, Washington, in a field trial established to evaluate asparagus cultivars for rust resistance (9). The area under the disease progress curve (AUDPC) for rust severity was used to select resistant and susceptible plants. Individual rust resistant male plants were selected from cultivars Delmonte 361 (plant D19), Jersey Giant (plant JG11), and Jersey Titan (plant T). Susceptible and moderately resistant male plants were selected from cultivars WSU-1 (plant W17) and Mary Washington (plant MW12), respectively. Moderately rust resistant female plants were selected from cultivars Jersey Giant (plant JG15) and Mary Washington (plant MW3); and the susceptible female clone Female 12 was selected. Jersey Giant was released as an all-male hybrid (6); but seed provided by J. H. Ellison (9) contained female plants, one of which was selected as plant JG15.

Plants were removed from the field, and their crowns were divided into several clones per plant. These clones were planted in 15-cm-diameter pots in the greenhouse. After plants had grown for at least 3 mo, crosses were made by hand pollination (4,16) using the three female and five male plants to produce 10 F_1 hybrid populations (Table 1). Seeds were extracted from mature berries (4), planted in the greenhouse, and grown for 7 mo. Natural light supplemented with daylight fluorescent lamps was used to provide a photoperiod of 16 hr/day for all plants grown in the greenhouse. Temperature ranged from 21 to 24 C during the day and from 17 to 21 C at night.

From 90 to 96 plants per hybrid population and the parents were transplanted on 5–6 April 1988 to a fine sandy loam soil at the Irrigated Agriculture Research and Extension Center near Prosser. Populations were planted in three- or four-row plots with a spacing of 30 cm between plants and 1.0 m between rows. Transplants were placed at a depth of 15–17 cm. Hybrid populations with the same female parent were planted in plots near each other. Plots were bordered by a rust-susceptible selection of Mary Washington to promote production of inoculum throughout the nursery. Sprinkler irrigation was used to irrigate plants and to encourage rust development. Rust originated from naturally occurring inoculum.

Rust severity was estimated as the proportion of surface area of each plant covered with uredinia by using Peterson's scale for cereal rust (17). Estimations were made six times in 1988, five times in 1989, and four times in 1990. The time between severity estimates ranged from 11 to 21 days and began on 17 July 1988, 18 July 1989, and 9 August 1990. All materials in a year were assessed on the same dates. The AUDPC was calculated for each plant to indicate the level of resistance to urediniospore infection (13).

Distribution of AUDPC values was examined in the 10 hybrid populations. Each data point was the mean value of an asparagus genotype over 3 yr. Distribution of each progeny population was tested against normal, lognormal, gamma, exponential, chi-square, and uniform distributions using chi-square goodness of fit statistics computed by a FORTRAN program (1).

Data for the asparagus populations were analyzed separately by analysis of variance for the 3 yr with genotypes as treatments. Assumptions of normality and homogeneity of variances of residuals were best satisfied by square-root transformation of data in all populations except Female 12 × Jersey Titan, which was analyzed without transformation. Differences among genotypes were further investigated by pairwise comparisons using Fisher's protected LSD.

Heritability was estimated as 2 times the regression coefficient, which was calculated from the weighted regression of offspring on each respective male parent to adjust for differences in number of progeny among the populations (15). Analysis of variance of the offspring data was used to determine the specific combining ability of the male parents in crosses with a common female parent.

Aecia developed on plants from naturally occurring inoculum in plots in the spring of 1989. The number of aecia per plant was determined for eight of the 10 populations. Correlation analysis was used to investigate any relationship between number of aecia and mean AUDPC for the 3 yr.

RESULTS

Severe rust epidemics developed on plants in the field during each of the 3 yr. Uredinia were evident on a majority of susceptible plants in mid-July 1988 and 1989 and in early August 1990. Rust severities on some plants in late October were 80% in 1988 and 1990, and 60% in 1989.

Mechanical and winter damage reduced stands in some populations, resulting in 80–94 surviving progeny in five populations, 41–50 in four populations, and 28 progeny in one population (Figs. 1 and 2). One or both parents died in three populations (Table 1).

Population means for AUDPC, based only on plants that survived 3 yr, ranged from 271 to 688 in the five crosses with Female 12, 229 to 356 in the three crosses with Mary Washington (MW3), and 377 to 411 in the two crosses with Jersey Giant (JG15). Most populations were skewed to the left (resistance), and the lognormal distribution provided a good fit in nine of the 10 populations (Table 1). Distribution of the population from the cross Female 12 × Jersey Titan was not significantly different from normality (Table 1). Frequency distributions are shown in Figures 1 and 2.

Variation in severity of rust associated with genotype was highly significant in all 10 populations. Parents differed significantly for rust severity in two crosses of susceptible × resistant (S × R) parents ($P = 0.01$). Differences between parents for the third S × R cross (Female 12 × Jersey Giant) could not be tested because Female 12 died after the first year in the field. Parents differed significantly for rust severity in a cross of susceptible × moderately resistant (S × MR) parents ($P = 0.05$) and in a cross of MR × R ($P = 0.05$) (Table 1). Parents did not differ significantly ($P > 0.05$) for the crosses MR × MR or S × S.

None of the progeny had AUDPC values significantly lower ($P > 0.05$) than the resistant parent or higher than the susceptible parent in the crosses of S × R (Female 12 × Delmonte 361 [D19], Female 12 × Jersey Giant [JG11], Female 12 × Jersey Titan [T]) or S × MR (Female 12 × Mary Washington [MW12]). Progeny did not have AUDPC values significantly lower than the resistant parent ($P = 0.05$) in crosses MR × R (Mary Washington [MW3] × Jersey Titan [T], Jersey Giant [JG15] × Delmonte 361 [D19]), but progeny had AUDPC values significantly higher ($P = 0.05$) than the MR parent in the cross Mary Washington (MW3) × Jersey Titan (T). Progeny had AUDPC values significantly lower and higher than parents ($P = 0.05$) in the populations from MR × MR (Mary Washington [MW3] × Mary Washington [MW12], Jersey Giant [JG15] × Mary Washington [MW12]) and S × S (Female 12 × WSU-1 [W17]).

The estimate of heritability for the nine populations in which the male parent survived the 3 yr in the field was 55% with a standard error of the mean of 80%. Jersey Giant (JG11) had a significantly greater ($P = 0.05$) specific combining ability than the other four male parents when crossed with Female 12 (Table 2). There was no difference ($P = 0.05$) in specific combining abilities for Mary Washington (MW12) and Delmonte 361 (D19) when they were crossed with either Female 12 or Jersey Giant (JG15) (Table 2).

Number of aecia per plant in 1989 was significantly correlated ($P = 0.05$) with mean AUDPC in three of the eight populations where aecia numbers were determined. Correlation coefficients were 0.23, 0.28, and 0.35 for the three populations with a significant relationship, and 0.01, 0.04, 0.06, 0.13, and 0.28 for the five with no relationship.

DISCUSSION

Resistance in asparagus infected with *P. asparagi* in the field in this study behaved as a quantitatively inherited

Table 1. Parental and population means for area under the disease progress curve (AUDPC), and best fitting distribution of 11 asparagus populations derived from crosses among asparagus clones susceptible, moderately resistant, and resistant to rust when infected with *Puccinia asparagi* in the field during 3 yr

Hybrid population[w]	Parental mean (AUDPC) Female	Parental mean (AUDPC) Male	Population mean (AUDPC)	Best fitting distribution	P-value[x]
Moderately resistant × resistant					
Mary Washington (MW3) × Jersey Titan (T)	313 ± 32[y]	46 ± 16	229 ± 21[y]	Lognormal	0.2114
Jersey Giant (JG15) × Delmonte 361 (D19)	–[z]	241 ± 65	377 ± 20	Lognormal	0.9477
Moderately resistant × moderately resistant					
Mary Washington (MW3) × Mary Washington (MW12)	197 ± 53	389 ± 23	341 ± 20	Lognormal	0.1562
Jersey Giant (JG15) × Mary Washington (MW12)	329 ± 85	378 ± 38	411 ± 27	Lognormal	0.9819
Susceptible × resistant					
Female 12 × Delmonte 361 (D19)	923 ± 165	122 ± 47	558 ± 30	Lognormal	0.6738
Female 12 × Jersey Giant (JG11)	–	42 ± 12	271 ± 22	Lognormal	0.6233
Female 12 × Jersey Titan (T)	1,135 ± 117	52 ± 14	516 ± 42	Normal	0.0745
Susceptible × moderately resistant					
Female 12 × Mary Washington (MW12)	991 ± 123	369 ± 69	610 ± 27	Lognormal	0.5963
Mary Washington (MW3) × WSU-1 (W17)	–	–	356 ± 23	Lognormal	0.6215
Susceptible × susceptible					
Female 12 × WSU-1 (W17)	837 ± 217	732 ± 111	688 ± 45	Lognormal	0.3006

[w] Female plant listed first for each cross. The same parent female or male clone for a cultivar was used for all crosses for that cultivar.
[x] This is a P = value for "lack of fit," i.e., the smaller the P-value, the greater the evidence that the distribution is different from that specified.
[y] Standard error of mean using nontransformed data.
[z] Parent died in the field planting.

trait, in that progeny were continuously distributed from low to high AUDPC values. Resistance in juvenile asparagus plants, as measured by the quantity of uredinia on stems, behaved similarly in the greenhouse in a previous study and was estimated to be conditioned by at least four or five genes (8). Slow rusting, the type of resistance in asparagus (9), is quantitatively inherited in other crops infected with rust (13,18,20,22).

The population means for AUDPC within a set of populations with a common female parent were least for populations with a resistant parent, next with a moderately resistant parent, and greatest when both parents were susceptible (Table 1). A significant skewing to the left (resistance) followed a lognormal distribution in nine of 10 populations. The skewing suggested dominant resistance.

Transgressive segregation for resistance, susceptibility, or both was found in four of the hybrid populations. However, a higher level of resistance than presently found in resistant parents (Jersey Giant [JG11], Delmonte 361 [D19], and Jersey Titan [T]) was not observed. Transgressive segregation for resistance was found in both crosses with two moderately resistant parents. The MR × MR population, Mary Washington (MW3) × Mary Washington (MW12), had as many highly resistant progeny as Mary Washington (MW3) × Jersey Titan (T), even though Jersey Titan (T) was resistant (Fig. 2). This was probably the result of the small population size of Mary Washington (MW3) × Jersey Titan (T), because Jersey Titan (T) had a significantly better specific combining ability than Mary Washington (MW3) (Table 2).

The estimate of heritability in this study was 55%, indicating that selection for resistance would be more effectual than was expected when estimates from the number of uredinia on asparagus seedlings after one generation of selection in the greenhouse was less than 20% (8). Variations in inoculation technique may have caused the low heritability estimates in that study (8,10). The large standard error of the mean for the heritability estimate in this study indicated considerable variability within lines in the field during the 3 yr. Estimates of heritability in other crops infected with rust have ranged from 13 to nearly 90% (13,18,20,22).

Asparagus cultivars consist of heterogeneous populations. Mary Washington and Delmonte 361 are open-pollinated cultivars; and WSU-1, Jersey Giant, and Jersey Titan are clonal hybrid cultivars from heterozygous parents. Variation for rust resistance has been reported within the resistant cultivars Jersey Giant, Jersey Centennial, Delmonte 361, and 44G × 22-8 (10). Resistant parents, except for Delmonte 361, had significantly greater ($P = 0.05$) specific combining abilities than moderately resistant and susceptible parents, indicating better potential performance of their progenies. Delmonte 361 (D19) was not significantly different from the moderately resistant parent, Mary Washington (MW12), and would probably be more properly classified as moderately resistant. Clones with relatively high levels of resistance in similar populations should be available for selection in breeding programs to develop asparagus cultivars and hybrids with rust resistance (10). Good progress has been previously made using this procedure (4,7,16).

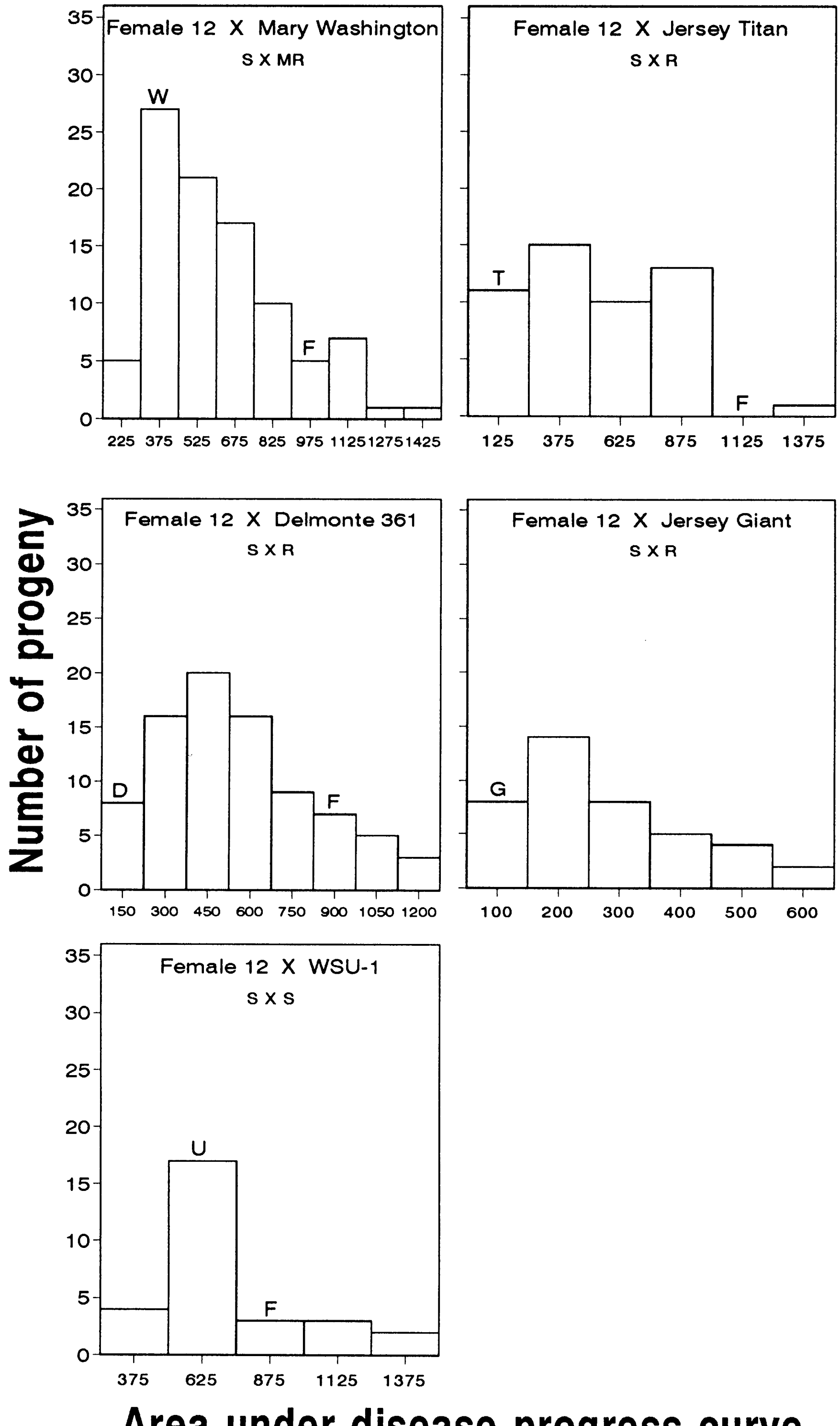

Fig. 1. Frequency distributions for the area under the disease progress curve of five asparagus hybrid F_1 populations infected with *Puccinia asparagi*. S = susceptible, MR = moderately resistant, and R = resistant. The letters F, D, T, G, W, and U indicate the respective classes in which the parent clones, Female 12, Delmonte 361 (D19), Jersey Titan (T), Jersey Giant (JG11), Mary Washington (MW12), and WSU-1 (W17), fall.

The AUDPC assumes all components of resistance are considered and proved to be reliable selection criteria in this and other studies (9,10). Multiple assessments for rust severity, as used to determine AUDPC, increase accuracy over single assessments for resistance in asparagus. This is because individual asparagus plants accumulate shoots of different ages as the season progresses, and shoots increase in resistance as they mature (8,9). Environmental conditions favoring infection and disease development were not uniform throughout the season, and some shoots received greater disease pressure than others. The multiple disease assessments summarized these cumulative effects over the season.

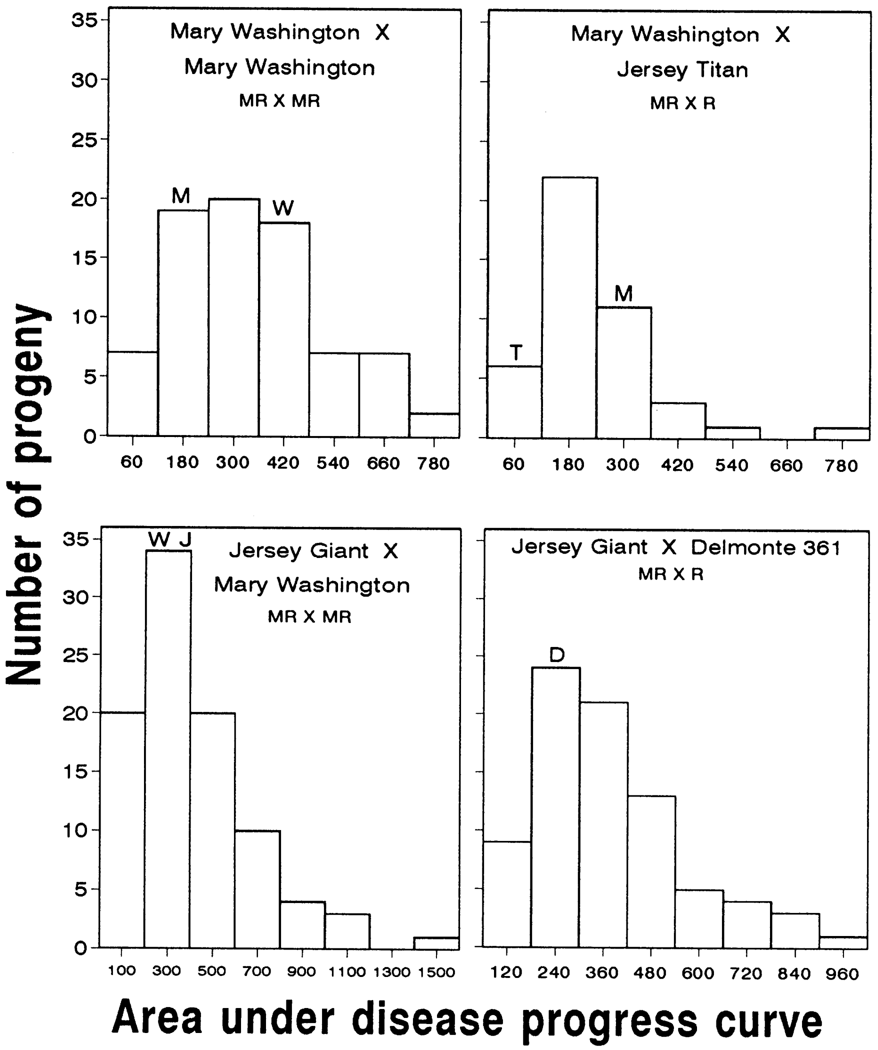

Fig. 2. Frequency distributions for the area under the disease progress curve of four asparagus F_1 populations infected with *Puccinia asparagi.* S = susceptible, MR = moderately resistant, and R = resistant. The letters M, W, T, J, and D indicate the respective classes in which the parent clones, Mary Washington (MW3), Mary Washington (MW12), Jersey Titan (T), Jersey Giant (JG15), and Delmonte 361 (D19), fall.

Table 2. Specific combining ability of five male parents when crossed with Female 12, three male parents when crossed with Mary Washington (MW3), and two male parents when crossed with Jersey Giant (JG15)

	Mean area under the disease progress curve[z]		
	Common female parent		
Male parent	**Female 12**	**Mary Washington (MW3)**	**Jersey Giant (J15)**
WSU-1 (W17)	640.1 a	316.8 a	...
Mary Washington (MW12)	552.2 ab	302.8 a	338.6 a
Delmonte 361 (D19)	445.2 bc	...	324.0 a
Jersey Titan (T)	436.8 c	193.2 b	...
Jersey Giant (JG11)	231.0 d	...	...

[z]Means based on square-root transformation of data detransformed after analysis. Within a column, values with the same letter are not significantly different (P = 0.05) according to Duncan's multiple range test.

Latent period and quantity of uredinia on stems calculated for asparagus cultivars in the greenhouse were related with AUDPCs of the cultivars in the field and would be effective in differentiating among cultivars for resistance (9–11). However, latent period and quantity of uredinia on stems were not as reliable a selection criterion as AUDPC (10).

Differences in rust resistance among asparagus genotypes were successfully determined in single-plant plots in this and another study (10). These plots were similar to the hill plots used to determine resistance to rust in small grains (13,21). However, AUDPC values calculated with rust severity estimates from plots with multiple plants are likely to be more accurate, because a wider range of shoots at varying ages is represented. Rust may be more severe in resistant plants established in hills than in those established in larger plots because of the nearness to inoculum produced on susceptible plants growing nearby (21). Small plots are appropriate when the number of clones of individual plants is limited. The small plots provide the opportunity to test a relatively large number of genotypes in a relatively small area under perhaps more uniform environmental conditions than when larger plots and land areas are used.

The number of aecia per plant was not expected to be highly related with the mean severity of uredinia on plants over the 3 yr. Quantitatively different responses to infection by urediniospores and basidiospores on asparagus genotypes have been noted previously (3,9, 11,16). Host resistance in asparagus to *P. asparagi* may be related to the nuclear condition (dikaryotic vs. haploid) of the infection spore (11).

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