Variation for Rust Resistance Within Asparagus Cultivars

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ABSTRACT

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Nine to 15 individual asparagus plants from each of five cultivars and one breeding line were selected for differences in latent period when infected with *Puccinia asparagi*. Plants were increased by crown division. Clones of five cultivars were tested for length of latent period and number of uredinia per linear centimeter of stem after being inoculated uniformly with *P. asparagi* in the greenhouse. Clones of six cultivars were tested for resistance as measured by the area under the disease progress curve (AUDPC) 2 yr in the field. Latent period varied significantly for clones within four cultivars, number of uredinia per linear centimeter of stem varied significantly for clones within only one cultivar, and AUDPC varied significantly for clones within all six cultivars both years. Latent periods of individual juvenile plants and AUDPC were not correlated, but mean latent periods of mature clones were negatively correlated with AUDPC in two of five cultivars and the combined cultivars. Number of uredinia per linear centimeter of stem was positively correlated with AUDPC in one of five cultivars. Values for AUDPC were significantly ($P = 0.01$) correlated the 2 yr. Considerable heterogeneity for rust resistance existed within open-pollinated and clonal hybrid asparagus cultivars. Progress in developing more highly resistant cultivars should be possible using selected germ plasm from commercial asparagus cultivars. The AUDPC of replicated asparagus clones in the field during severe rust epidemics would be beneficial in selecting for resistance.

Resistance in asparagus (*Asparagus officinalis* L.) to rust (*Puccinia asparagi* DC.) has been known for many years. Since the early 1900s efforts have been directed toward identifying and using resistance in asparagus to manage rust (2,5,9,11,19). However, the only type of resistance found in the genus *Asparagus* has been quantitative (rather than qualitative) differences in the intensity of infection (1,5,6,9,19). In Washington State, asparagus cultivars Jersey Giant, Jersey Centennial, Delmonte 361, and UC-157 rusted more slowly in the field and had longer latent periods and fewer uredinia per square centimeter of stem when inoculated uniformly with urediniospores in the greenhouse than did cultivars Glen Smith's Mary Washington, Wash T2, and WSU-1 (6).

Considerable variation for several traits has been observed among plants of clone- and seed-propagated asparagus cultivars (18). Differences for rust resistance among plants within open-pollinated asparagus cultivars have been noted in commercial fields in Washington State (*unpublished*). The purpose of this study was to quantify the degree of variation for rust resistance within the five asparagus cultivars WSU-1, Glen Smith's Mary Washington, Delmonte 361, Jersey Giant, Jersey Centennial, and 44G × 22-8, a breeding line.

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MATERIALS AND METHODS

Seed of WSU-1 and Delmonte 361 was received from the Washington Asparagus Growers Association, Sunnyside, WA; seed of Glen Smith's Mary Washington was produced by Glen Smith, Sunnyside, WA; and seed of Jersey Giant, Jersey Centennial, and 44G × 22-8 came from J. H. Ellison, Rutgers University, New Brunswick, NJ. Seed was germinated on moistened filter paper in petri dishes at 25 C and planted in a silt loam soil, two plants per 8-cm-diameter pot, in a greenhouse. When 50–75% of the cladophylls appeared (5) on the third shoot to emerge, plants in 19 pots of each cultivar were inoculated as they rotated on a platform by spraying them as uniformly as possible with an atomized oil suspension of urediniospores of *P. asparagi* as described previously (6). Experimental design was a randomized complete block with 19 replicates. Latent period and infection frequency were determined and compared among the cultivars and have been reported (6).

Within each of the six cultivars, between nine and 15 plants representing a gradient in length of latent period within a cultivar were selected (Tables 1–6) and replanted in 16-cm-diameter pots in a 1:1 mixture of silt loam soil and peat moss mix. These plants were grown and reproduced asexually by crown division in the greenhouse over a 24-mo period until four to six individuals per genotype were obtained. Plants were fertilized monthly with 0.15 g per pot of 34-0-0 NH_4NO_3 to encourage bud development and to build up carbohydrate reserves in the crown. Foliage was then removed to stimulate new shoot emergence before inoculation.

Urediniospores were originally collected from an asparagus field near Pasco, WA, and increased from a single uredinium on WSU-1 in the greenhouse. Urediniospores increased for inoculation were collected the day of inoculation with a mini-cyclone spore collector (3). When new primary shoots of a cultivar were in the 50–75% cladophyll stage of development (5), they were inoculated with *P. asparagi*. Plants of a cultivar or line were inoculated on three or four different days in a completely random design with three to six replicates per cultivar so that shoots of a similar age were inoculated. The number of plants inoculated was 29 for WSU-1, 43 for Glen Smith's Mary Washington, 39 for Delmonte 361, and 51 each for Jersey Giant and Jersey Centennial. One side of a central 60-cm section of the primary shoot of each plant was inoculated separately with 0.3 ml of an oil suspension (Soltrol 170) of approximately 7×10^5 urediniospores per milliliter. Urediniospores were in a size 00 gelatin capsule and were applied with a spore-oil suspension atomizer (3) at an air pressure of 60 kPa. Plants were placed in a mist chamber for 24 hr, then returned to the greenhouse. Natural light supplemented with fluorescent lamps was used to provide a photoperiod of 15 hr per day. Temperature ranged from 21 to 24 C during the day and from 17 to 21 C at night.

After inoculation, uredinia from initial points of infection (9) were counted when the red-orange of a pustule was visible to the unaided eye on primary shoots every day for 10 days and then on alternate days for 6 more days. Latent period was taken as the number of days from inoculation until 50% of uredinia appeared and was calculated from linear regression of probit percent uredinia appeared on days after inoculation as described by Shaner (16). The number of uredinia per linear centimeter of shoot length was calculated from the total number of uredinia on a primary shoot divided by 60 cm.

Nine to 15 clones of each of the five cultivars and one breeding line of the same plants used in experiments in the greenhouse were transplanted during

April 1987 into a fine sandy loam soil at the Irrigated Agriculture Research and Extension Center near Prosser, WA. Transplants were spaced 30 cm apart within a row, and rows were 1.5 m apart. The trial design was a randomized complete block of one plant per plot with four replicates. Plants were irrigated by sprinkler, which also encouraged rust development. The planting was bordered with the rust-susceptible asparagus cultivar WSU-1, which was infected with uredinia in 1986 and had aecia the springs of 1987 and 1988.

Rust severity was estimated as the proportion of surface area of the foliage of each plant covered with uredinia, using the modified Cobb scale for cereal stem rust (15). Rust severity was estimated five times in 1987 and five times in 1988 at 10–17 day intervals, beginning 28 July in 1987 and 19 July in 1988. The area under the disease progress curve (AUDPC) was calculated as previously described (7) for each plant. Analysis of variance using a model for an unbalanced design was conducted for latent period and number of uredinia data, and a model for a balanced design was used for AUDPC data. Duncan's new multiple range test was used to compare means.

Linear correlation was used to compare the relationship between either latent period or number of uredinia per square centimeter of stem of the individual plants initially selected and with the mean values for clones measured in the replicated tests. Linear correlation

Table 1. Latent period and number of uredinia for 10 single plants of asparagus cultivar WSU-1 and of clones from the same plants and the area under the disease progress curve (AUDPC) of the clones in the field when infected with *Puccinia asparagi*

	Single plants[w]		Clones[x]			
	Latent period	Uredinia	Latent period[y]	Uredinia per	AUDPC[z]	
Plant	(days)	per cm²	(days)	linear cm[y]	1987	1988
W-10 A	9	0.8	···	···	114 a	200 a
W-8 B	9	0.9	9.6 a	0.08 a	378 a	401 ab
W-1 A	8	2.5	···	···	986 b	662 b
W-7 B	8	4.2	···	···	1,001 b	1,582 c
W-13 A	9	3.2	9.3 a	0.13 a	1,005 b	634 b
W-15 B	9	0.8	8.3 ab	0.09 a	1,367 bc	1,740 c
W-14 B	9	1.0	8.2 ab	0.25 a	1,621 cd	1,686 c
W-7 A	8	5.4	8.1 ab	0.16 a	1,657 cd	988*
W-16 A	8	2.2	8.6 ab	0.09 a	1,972 d	1,744 c
W-17 A	9	0.4	7.5 b	1.56 b	2,420*	2,057**
Standard error of mean			0.17	0.035	188	130

[w] Selected unreplicated plants representing a gradient in length of latent period within the cultivar (6).
[x] Within a data column, values with the same lowercase letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[y] Values are means of three to six replications.
[z] Values are means of four replications. * = Mean of two replicates and ** = mean of one replicate; values are not included in analysis of variance.

Table 2. Latent period and number of uredinia for 11 single plants of asparagus cultivar Glen Smith's Mary Washington and of clones from the same plants and the area under the disease progress curve (AUDPC) of the clones in the field when infected with *Puccinia asparagi*

	Single plants[w]		Clones[x]			
	Latent period	Uredinia	Latent period[y]	Uredinia per	AUDPC[z]	
Plant	(days)	per cm²	(days)	linear cm[y]	1987	1988
M-2 A	9	1.3	9.6 ab	0.08	195 a	347 ab
M-9 A	8	4.0	10.1 a	0.02	202 a	176 a
M-10 A	9	1.9	7.7 c	0.14	347 ab	569 ab
M-1 A	9	2.7	8.6 bc	0.06	417 ab	196 a
M-4 A	9	0.2	···	···	534 b	520 ab
M-18 B	8	1.0	8.7 abc	0.10	550 b	822 bc
M-12 A	8	6.2	7.6 c	0.19	574 bc	893 bc
M-17 B	9	0.7	8.4 bc	0.43	770 c	1,896 c
M-2 B	8	1.3	8.8 abc	0.16	1,003 d	1,318 cd
M-19 A	8	2.5	8.5 bc	0.10	1,023 d	1,563 bc
M-14 A	9	4.6	···	···	2,016 e	1,696 bc
Standard error of mean			0.14	0.035	72	174

[w] Selected unreplicated plants representing a gradient in length of latent period within the cultivar (6).
[x] Within a data column, values with the same lowercase letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[y] Values are means of three to six replications.
[z] Values are means of four replications.

Table 3. Latent period and number of uredinia for nine single plants of asparagus cultivar Delmonte 361 and of clones from the same plants and the area under the disease progress curve (AUDPC) of the clones in the field when infected with *Puccinia asparagi*

	Single plants[w]		Clones[x]			
	Latent period	Uredinia	Latent period[y]	Uredinia per	AUDPC[z]	
Plant	(days)	per cm²	(days)	linear cm[y]	1987	1988
D-2 B	9	0.5	8.7 bcd	0.17	223 a	305 a
D-5 A	12	0.1	10.5 a	0.13	271 a	479 abc
D-8 A	8	0.9	10.4 a	0.05	625 b	375 ab
D-8 B	9	2.2	9.3 b	0.10	640 b	625 cd
D-16 B	10	0.4	8.7 bcd	0.07	731 b	866 d
D-12 A	12	0.4	8.0 d	0.11	940 bc	847 d
D-9 B	9	0.2	9.0 bc	0.02	1,040 c	550 bc
D-10 B	11	0.6	8.2 cd	0.14	1,608 d	1,513 e
D-15 B	9	2.1	8.5 bcd	0.50	1,864 d	1,521 e
Standard error of mean			0.10	0.031	100	71

[w] Selected unreplicated plants representing a gradient in length of latent period within the cultivar (6).
[x] Within a data column, values with the same lowercase letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[y] Values are means of three to six replications.
[z] Values are means of four replications.

Table 4. Latent period and number of uredinia for 12 single plants of asparagus cultivar Jersey Giant and of clones from the same plants and the area under the disease progress curve (AUDPC) of the clones in the field when infected with *Puccinia asparagi*

	Single plants[w]		Clones[x]			
	Latent period	Uredinia	Latent period[y]	Uredinia per	AUDPC[z]	
Plant	(days)	per cm²	(days)	linear cm[y]	1987	1988
JG-19 B	11	0.6	9.2 abc	0.05	52 a	154 a
JG-2 A	9	0.8	9.8 abc	0.06	83 ab	298 ab
JG-18 B	11	0.2	9.2 abc	0.02	150 ab	239 ab
JG-17 B	11	0.1	9.9 ab	0.03	153 ab	535 bc
JG-13 A	13	0.2	10.6 a	0.05	262 bc	689 c
JG-8 A	10	1.1	10.0 ab	0.05	273 bc	673 c
JG-16 B	8	1.1	8.2 bc	0.10	435 cd	824 cd
JG-13 B	8	1.2	9.7 abc	0.07	438 cd	853 cd
JG-14 A	9	0.9	9.2 abc	0.02	470 d	1,355 ef
JG-14 B	10	0.2	8.2 bc	0.10	523 d	1,351 ef
JG-9 A	9	0.6	8.5 abc	0.04	585 d	1,141 de
JG-18 A	9	0.7	7.8 c	0.09	896 c	1,633 f
Standard error of mean			0.14	0.009	65	115

[w] Selected unreplicated plants representing a gradient in length of latent period within the cultivar (6).
[x] Within a data column, values with the same lowercase letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.
[y] Values are means of three to six replications.
[z] Values are means of four replications.

was also used to determine the relationship between either length of latent period or number of uredinia per linear centimeter of stem measured in the greenhouse and AUDPC measured in the field.

RESULTS

Significant differences ($P = 0.05$) for mean latent period among clones were found within WSU-1, Glen Smith's Mary Washington, Delmonte 361, and Jersey Giant but not within Jersey Centennial (Tables 1–5). A significant difference ($P = 0.05$) among clones for uredinia per linear centimeter of shoot was found only within WSU-1 (Tables 1–5).

A severe rust epidemic developed on plants in the field both years. In 1987, the first mean disease severity ratings on 28 July for clones of WSU-1 ranged from 0 to 10% and the final mean ratings ranged from 10 to 90%. For clones of Jersey Giant, the first mean severity ratings ranged from 0 to 3% and the final, from 5 to 40%. In 1988, the first mean severity ratings for clones of WSU-1 ranged from 0 to 5% and the final, from 10 to 80%. For clones of Jersey Giant in 1988, the first mean severity rating ranged from 0.1 to 4% and the final, from 10 to 40%. AUDPC among clones varied significantly ($P = 0.05$) within all six cultivars (Tables 1–6). Values for AUDPC of each cultivar the 2 yr were significantly ($P = 0.01$) correlated (Table 7).

Latent period measured on individual plants in the greenhouse was not significantly correlated with the mean latent period of clones developed from those plants or with the AUDPC of clones in the field. Number of uredinia of single selected plants was not related to number of uredinia of clones. Number of uredinia of clones was significantly ($P = 0.05$) correlated with AUDPC of only Glen Smith's Mary Washington in 1988 (Table 7). Latent periods of WSU-1 and Jersey Giant clones were significantly correlated ($P = 0.01$ and 0.05, respectively) with AUDPC of the clones in the field, but latent periods of the other three cultivars were not significantly correlated with AUDPC (Table 7). Both the latent period and the number of uredinia per linear centimeter of stem of clones of the five cultivars combined were significantly correlated ($P = 0.01$) with AUDPC (Table 7).

DISCUSSION

Variation for rust resistance within asparagus cultivars was expected, since asparagus cultivars consist of heterogeneous populations. Glen Smith's Mary Washington and Delmonte 361 are open-pollinated cultivars and WSU-1, Jersey Giant, Jersey Centennial, and 44G × 22-8 are clonal hybrid cultivars from heterozygous parents. Considerable variation for several traits has been shown to exist among plants of clonal hybrid and open-pollinated asparagus cultivars (18). Strains of the cultivars Mary Washington and Paradise from different areas of the United States developed significantly different numbers of uredinia when inoculated in the greenhouse (5). In the present study, the magnitude of variation for AUDPC was large for all cultivars. Both relatively resistant and susceptible individuals were identified within both the susceptible cultivars WSU-1 and Mary Washington and the resistant cultivars Delmonte 361, Jersey Giant, Jersey Centennial, and line 44G × 22-8 (Tables 1–6). It would be possible therefore to select for resistance or susceptibility in these cultivars. Jersey Centennial—a clonal hybrid between rust-resistant male and female plants selected from Mary Washington—is an example of selection for resistance (4).

In addition to the effect of disease resistance, the heterogeneous mixture of rust-resistant plants within resistant cultivars of asparagus may produce an effect similar to cultivar mixtures in restricting the spread of a pathogen in a crop (23). Slow-rusting resistance may provide more durable control of rust than hypersensitive resistance (22). The heterogeneity within slow-rusting cultivars of asparagus may exert less selection pressure on the pathogen population to overcome various components of slow-rusting resistance (long latent period, few uredinia) in the host than in cultivars consisting of clones of slow-rusting plants. Physiologic races of *P. asparagi* have never been identified (5). The use of cloned asparagus plants to establish production fields of genetically similar plants may result in development of physiologic races of *P. asparagi*.

Selection for quantitative types of resistance is often thought to be difficult, especially when single plants are selected or when seedlings are screened (14). Latent period has been used as a criterion for selecting slow-rusting resistance in

Table 5. Latent period and number of uredinia for 15 single plants of asparagus cultivar Jersey Centennial and of clones from the same plants and the area under the disease progress curve (AUDPC) of the clones in the field when infected with *Puccinia asparagi*

	Single plants[w]		Clones[x]			
	Latent		Latent	Uredinia	AUDPC[z]	
Plant	period (days)	Uredinia per cm^2	period[y] (days)	per linear cm[y]	1987	1988
JC-16 A	9	0.3	8.5	0.05	203 a	434 ab
JC-4 B	10	0.3	10.0	0.03	220 a	453 ab
JC-9 A	10	0.6	···	···	240 ab	315 a
JC-2 B	9	1.0	9.2	0.05	253 ab	258 a
JC-5 A	9	1.5	8.6	0.19	263 ab	628 abc
JC-1 A	9	2.0	···	···	343 ab	337 a
JC-10 A	9	0.5	8.9	0.12	376 ab	455 ab
JC-13 B	8	2.0	8.4	0.11	382 ab	437 ab
JC-16 B	10	0.9	8.8	0.04	384 ab	489 abc
JC-14 A	10	0.3	···	···	589 bc	962 cde
JC-17 A	10	0.4	8.5	0.13	765 cd	889 bcde
JC-4 A	11	1.2	10.0	0.08	780 cd	1,228 e
JC-12 A	9	1.3	8.1	0.28	906 cd	685 abcd
JC-19 B	10	0.8	8.7	0.15	933 d	1,198 e
JC-15 B	11	0.5	8.8	0.09	1,022 d	1,102 de
Standard error of mean			0.14	0.016	108	150

[w] Selected unreplicated plants representing a gradient in length of latent period within the cultivar (6).
[x] Within a data column, values with the same lowercase letter are not significaty different ($P = 0.05$) according to Duncan's multiple range test.
[y] Values are means of three to six replications.
[z] Values are means of four replications.

Table 6. Latent period and number of uredinia for shoots of 10 single plants of asparagus line 44G × 22-8 and the area under the disease progress curve (AUDPC) in the field of clones from the same plants when infected with *Puccinia asparagi*

	Single plants[y]			
	Latent		AUDPC of clones[z]	
Plant	period (days)	Uredinia per cm^2	1987	1988
G-8 B	9	2.0	236 a	247 a
G-14 A	9	1.2	246 a	159 a
G-14 B	12	0.5	291 a	181 a
G-1 B	10	0.9	414 ab	349 ab
G-13 B	9	1.5	662 abc	360 ab
G-19 A	9	0.7	668 abc	711 cd
G-7 A	10	0.8	767 bcd	559 bc
G-18 B	9	1.0	836 bcd	867 d
G-9 B	8	7.6	987 cd	1,150 e
G-2 A	9	0.7	1,130 d	1,239 e
Standard error of mean			139	73

[y] Selected unreplicated plants representing a gradient in length of latent period within the line 44G × 22-8 (6).
[z] Within a data column, values with the same lowercase letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test. Values are means of four replicates.

Table 7. Correlation coefficients for relationships between area under the disease progress curve (AUDPC) of asparagus clones from six cultivars and the cultivars combined in 1987 and 1988 and length of latent period and number of uredinia of selected single plants and of clones when infected with *Puccinia asparagi*

Cultivars AUDPCs	AUDPC, 1988	Single plants		Clones	
		Latent period (days)	Uredinia per cm²	Latent period (days)	Uredinia per linear cm
WSU-1					
AUDPC, 1987	0.85**[z]	−0.19	0.05	−0.89**	0.65
AUDPC, 1988	···	−0.10	−0.11	−0.83**	0.53
Mary Washington					
AUDPC, 1987	0.77**	0.04	0.25	−0.36	0.43
AUDPC, 1988	···	−0.07	−0.01	−0.38	0.76*
Delmonte 361					
AUDPC, 1987	0.92**	−0.02	0.38	−0.56	0.58
AUDPC, 1988	···	0.23	0.34	−0.61	0.62
Jersey Giant					
AUDPC, 1987	0.94**	−0.48	0.22	−0.70*	0.48
AUDPC, 1988	···	−0.41	0.15	−0.60*	0.40
Jersey Centennial					
AUDPC, 1987	0.85**	0.52*	−0.07	−0.18	0.47
AUDPC, 1988	···	0.68**	−0.21	0.11	0.25
44G × 22-8					
AUDPC, 1987	0.94**	−0.47	0.32	···	···
AUDPC, 1988	···	−0.53	0.42		
Cultivars combined					
AUDPC, 1987	0.80**	−0.21	0.27	−0.51**	0.60**
AUDPC, 1988	···	−0.16	0.14	−0.50**	0.49**

[z] * and ** = Statistical significance of $P = 0.05$ and 0.01, respectively.

the greenhouse (6,7,14,20). In an earlier study, the mean latent period and number of uredinia calculated for asparagus cultivars in the greenhouse were related to AUDPC of the cultivars in the field (6). In this study, mean length of latent period of clones and AUDPC were correlated when data for cultivars were combined. Mean latent period would be effective in differentiating among cultivars for resistance. However, selecting individual plants within cultivars based on length of latent period would not have been effective in finding resistance in the field to rust. Length of mean latent period of clones was related to AUDPC in the field within only two of the five cultivars tested. Hence, mean latent period of clones would be effective in selecting for resistance only within these two cultivars. A difference between the two tests for latent period is that the single plant selections were made with juvenile plants and the clones were mature plants that had previously produced flowering shoots. The relative length of latent periods of juvenile plants or seedlings of wheat and barley has been shown to represent either the relative length of latent period of mature plants or resistance in the field in some rust studies (12,14,20) but not in others (10,13). The lack of correlation between mean latent period measured on the clones and AUDPC measured on these same clones in the field for three of the five test cultivars suggests that components of slow rusting, in addition to latent period, may have an important effect on disease development in the field.

In the study reported here, initial selections were not based on infection frequency, so it cannot be determined if numbers of uredinia within a cultivar would be a valid selection criterion for asparagus. Mean number of uredinia of clones and AUDPC were significantly ($P = 0.01$) correlated when data for cultivars were combined. Variations in technique of inoculating asparagus with *P. asparagi* may produce many infections on relatively resistant plants (5). A technique to apply inoculum uniformly is essential to successfully select for rust resistance using greenhouse procedures.

The single plant plots in the field were successfully used to differentiate rust-susceptible and rust-resistant asparagus lines. These plots were similar to hill plots used to determine resistant lines of wheat (21), barley (6–8), and oats (17) to rust. A disadvantage with a single plant plot of asparagus is that if a plant dies, a missing plot and hence missing information result. Rust may be more severe in slow-rusting plants in hills than in larger plots because the slow-rusting plants are continuously showered with inoculum from susceptible plants growing nearby (8,21). Small plots are advantageous when individuals of a clone are limited. They give the opportunity to test a relatively large number of clones in a relatively small area under perhaps more uniform environmental conditions than when larger plots and land areas are used.

Differences among clones within all six cultivars were detected in the field using AUDPC. Differences for rust resistance among strains of adapted asparagus cultivars are important because the strains will usually contain cultivar characteristics for adaptibility. The AUDPC was the most reliable selection criterion used in this study. Progress could be made in breeding work by selecting slow-rusting clones within commercial cultivars in the field with low AUDPC values.

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