# Occurrence and Distribution of Virulence in *Puccinia coronata* var. avenae in Europe, 1977-1980

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#### ABSTRACT

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Infection of oats (Avena sativa) by Puccinia coronata var. avenae is generally widespread over Europe, with the most severe infections occurring in the southern portion of the continent. From 1977 to 1980, crown rust isolates were obtained from various regions of Europe, and their virulence was determined on lines of A. sativa that contain known genes (Pc) for crown rust resistance. From 1977 to 1979, 12 lines were used as differentials; in 1980, 14 lines were used. In 1977-1979, 122 crown rust isolates from Austria, Czechoslovakia, Poland, Soviet Union/Lithuania, Soviet Union/northwestern, and Yugoslavia comprised 50 virulence combinations. In 1980, 176 isolates from Austria. Czechoslovakia. Federal Republic of Germany, Denmark, Italy, Poland, Portugal, and Switzerland comprised 75 virulence combinations. These results indicate the very high variability of virulence in the European isolates of P. coronata var. avenae. The distribution of virulence on the host resistance genes varied, depending on the region from which the isolates of P. coronata var. avenae were obtained. In general, the most ineffective genes in oats were Pc 35, 40, 45, 46, 47, and 54, whereas the most effective genes were Pc 39, 48, 50, and 55. The effectiveness of the remaining genes varied from poor to good, depending on the region. Limited data indicate that genes Pc 58 and 59 are highly effective. The usefulness of the Pc genes used in the study in relation to breeding oats for resistance in P. coronata var. avenae is discussed.

Crown rust of oats (Avena sativa L.), caused by Puccinia coronata Cda. var. avenae Fras. & Led., is a widespread disease occurring in most parts of the world where oats are cultivated. In 1934, Blattny (1) estimated the decrease in oat yield in Czechoslovakia to be 3.000-4.000 railway carloads. In Poland, Ralski and Muszynska (8) indicated that crown rust was particularly harmful to late-maturing cultivars and late-sown fields. According to Kostic (6), crown rust has probably been the most destructive pathogen of oats in Yugoslavia, particularly at lower elevations and along riverbanks. Since the European Oat Disease Nursery was established in 1969, crown rust has been shown to occur in central and southeastern Europe each year (13). The infections have ranged from light to severe, depending on location and climatic conditions.

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Oat cultivars with crown rust resistance are not in widespread use in Europe. However, collections of A. sterilis L. from the Mediterranean region have yielded a broad range of crown rust resistance (7,14), from which a number of genes conferring resistance to P. coronata var. avenae have been isolated (14). These genes have formed the basis of breeding for resistance to crown rust in North America.

In breeding oats resistant to crown rust, the sources of resistance must be selected carefully, and the resulting cultivars should contain several different genes for resistance. The selection of resistance sources depends on a knowledge of the virulence characteristics of the P. coronata var. avenae population in those areas for which resistant cultivars are to be produced. To provide a rational basis for the choice of resistance sources for Europe, the virulence of the P. coronata var. avenae population needed to be assessed based on potentially useful genes for breeding crown rust-resistant cultivars for this region. Beginning in 1977, crown rust isolates from various regions in Europe were assessed using a set of oat lines carrying single genes (Pc) for resistance to P. coronata var. avenae similar to those used in Canada (4,5). This paper reports on the progess of this

research and indicates which of the resistance genes may be the most useful. Preliminary studies of physiologic specialization of *P. coronata* var. *avenae* in eastern Europe have been reported (9-12).

# **MATERIALS AND METHODS**

Samples of *P. coronata* var. avenae were collected from farm fields of cultivated oats, from wild oats (A. fatua L.), and from nurseries consisting of various lines of oats. The countries or regions from which rust samples were obtained are indicated in Tables 1-3.

Urediospores were transferred to the susceptible cultivars Victory or Tiger, after which one single-pustule isolate was made from each collection, increased, and used to inoculate a set of differential lines to determine the virulence characteristics of each isolate. The differential lines, except as noted, are backcross lines of the cultivar Pendek, possessing single genes (Pc) for resistance to crown rust. All genes used were derived from A. sterilis.

In 1977-1979, 12 oat lines were used as differentials; in 1980, two more lines were added. In addition, in 1980, four more lines containing either the genes Pc 58 (TAM 301), 59 (TAM 312), 60 (Coker 227), or 61 (Coker 234) were used in the assessment of virulence of isolates from Italy, Portugal, Switzerland, Federal Republic of Germany, Denmark, Austria, Czechoslovakia, Soviet Union (Lithuania), Poland, and Yugoslavia. These lines do not appear in the virulence formulas in Table 2, but they were included in the calculations of frequencies of virulence. The rust isolates were differentiated into virulence/avirulence combinations (see Tables 1 and 2) using the formula method of Green (3). Work by the senior author was conducted at the Research Institute of Crop Protection in Prague, Czechoslovakia, and by the second author at the University of Konstanz, Federal Republic of Germany.

## **RESULTS AND DISCUSSION**

Occurrence and distribution. In 1980, crown rust was light in central and

northern Europe because of a late cool season. Infection became general only after much of the crop was nearly mature.

Pathogenic specialization. During 1977 through 1979, 122 isolates from Austria, Czechoslovakia, Poland, Soviet Union/Lithuania, Soviet Union/ northwestern, and Yugoslavia comprised 50 virulence combinations using the 12 Pc-gene lines as differentials (Table 1). In 1980, 176 isolates from Austria, Czechoslovakia, Federal Republic of Germany, Denmark, Italy, Poland, Portugal, and Switzerland comprised 75 virulence combinations on 14 Pc-gene lines (Table 2). Many of the virulence combinations in Tables 1 and 2 may be similar, but they are not directly comparable because of the two additional differential Pc-gene lines used in 1980.

The data in Tables 1 and 2 indicate the very high variability of virulence in P. coronata var. avenae. In many instances, a virulence combination is represented by only one isolate. The data do not indicate that any particular virulence combination predominates in any region. Despite the large number of virulence combinations obtained, the full range of variability in virulence has apparently not been assessed. For example, from Portugal in 1980, 29 isolates comprised 22 virulence combinations (Table 2). Clearly, many more isolates are needed to realize the full range of virulence in P. coronata var. avenae over all of Europe.

Crown rust is widely distributed in southern Europe, and the data in Table 2 from Italy and Portugal also indicate a very wide range of virulence in these areas based on the differentials used. From Portugal, only a few isolates were virulent on five or fewer Pc-gene lines, whereas most isolates were virulent on six or seven Pc-gene lines. For comparison, most isolates from the Federal Republic of Germany were virulent on three or fewer Pc-gene lines. A calculation of the mean virulence capabilities of the P. coronata var. avenae populations resulted in a value of 1.6 for the Federal Republic of Germany and 6.3 for Portugal (Table 2). This indicates that on average the Portuguese isolates carry about five times as many genes for virulence as do those from the Federal Republic of Germany, as determined by the differentials used. In general, the isolates from southern Europe, including Yugoslavia, appear to carry more genes for virulence on the Pclines used than do those from eastern, central, and northern Europe, as indicated by their mean virulence capabilities (Tables 1 and 2).

The virulence combinations in Tables 1 and 2 indicate the range of virulence but are of limited use in assessing the *Pc* genes as sources of crown rust resistance in oat breeding. To obtain this information, the distribution of frequency of virulence on each of the *Pc*-gene lines was calculated and given as the percentage of the total

number of isolates from each country or region that showed virulence on each of the Pc-gene lines (Table 3). Few isolates were avirulent on all of the Pc-gene lines. The largest percentage of avirulent isolates was found in the Federal Republic of Germany and Switzerland, with 23.0 and 21.4%, respectively. However, resistance genes in oats are available that are effective against the populations of P. coronata var. avenae in all regions of Europe.

A useful concept in the management of plant disease is a regionally based diversification of crown rust resistance genes within an epidemiologic region where exchange of inoculum may occur (2). This system has merit provided that sufficient crown rust resistance genes are available for deployment. Crown rust is well suited for management by this method because a large pool of crown rust resistance genes is available. Careful selection and deployment of combinations of genes conferring resistance to *P. coronata* var. avenae would be a positive step in controlling crown rust in Europe.

The distribution of virulence on the *Pc*-gene lines used in this study indicates considerable regional specialization of virulence (Table 3), although more extensive studies over a longer period of time are required for a full assessment. Over most of central Europe, the

**Table 1.** Virulence combinations of isolates of *Puccinia coronata* var. *avenae* from Austria (A), Czechoslovakia (CS), Poland (P), Soviet Union/Lithuania (SU/L), Soviet Union/northwestern (SU), and Yugoslavia (YU) on lines of *Avena sativa* containing known genes (*Pc*) for crown rust resistance in 1977–1979

Virulence combination (effective/ineffective)	Number of isolates						
of host resistance (Pc) genes	A	CS	P	SU/L	SU	ΥU	
35,38,39,40,45,46,47,48,50,54,55,56/		1	4		1		
38,39,40,45,46,47,48,50,54,55,56/35	5	3	6	•••	5		
35,39,40,45,46,47,48,50,54,55,56/38	1		1	1	•••		
35,38,39,45,46,47,48,50,54,55,56/40	1			•••	•••		
5,38,39,40,45,46,47,48,50,54,55/56			1				
9,40,45,46,47,48,50,54,55,56/35,38	1	4	3		2		
8,39,45,46,47,48,50,54,55,56/35,40		1		•••	-		
8,39,40,46,47,48,50,54,55,56/35,45	1		1				
18,39,40,45,46,47,48,50,54,55/35,56		1	1		1		
	•••		1	•••			
5,39,40,46,47,48,50,54,55,56/38,45							
55,39,40,45,46,47,48,50,54,55/38,56				1			
5,38,39,46,47,48,50,54,55,56/40,45	•••	2	•••	•••	•••	•••	
5,38,39,40,47,48,50,54,55,56/45,46		1	•••	•••		•••	
9,45,46,47,48,50,54,55,56/35,38,40	3	•••	•••	2	2	•••	
9,40,46,47,48,50,54,55,56/35,38,45	•••	2	1	•••	•••	•••	
9,40,45,46,47,50,54,55,56/35,38,48	•••	1	•••	•••	•••	•••	
9,40,45,46,47,48,50,55,56/35,38,54	. 1	•••	•••	•••	•••	•••	
9,40,45,46,47,48,50,54,55/35,38,56	•••	•••	1	2	1	•••	
18,39,45,46,47,48,54,55,56/35,40,50	•••	•••	•••	1	•••	•••	
8,39,40,45,46,48,50,54,55/35,47,56	•••	•••	•••	•••	1		
5,38,39,45,46,47,48,54,55/40,50,56		•••		1			
5,38,39,40,45,46,50,55,56/47,48,54	•••	1					
9,40,46,47,48,50,54,55/35,38,45,56			1				
88,39,46,48,50,54,55,56/35,40,45,47				•••	3	1	
8,39,45,46,48,50,55,56/35,40,47,54	1						
88,39,40,48,50,54,55,56/35,45,46,47		1					
15,39,40,45,46,50,54,55/38,47,48,56	•••	1	•••				
	3	i	•••	•••	•••		
35,33,39,48,50,54,55,56/40,45,46,47							
35,38,39,47,48,50,55,56/40,45,46,54			1				
35,38,39,46,48,50,55,56/40,45,47,54	2	1		•••	1		
35,38,39,45,48,50,55,56/40,46,47,54	1	•••	3	•••	•••		
35,38,39,45,46,50,55,56/40,47,48,54	•••	1	•••	•••	•••	•••	
35,38,39,40,48,50,55,56/45,46,47,54	1	•••	•••	•••	•••	•••	
35,38,39,40,47,50,55,56/45,46,48,54	•••	•••	1	•••	•••	•••	
35,38,39,40,46,50,55,56/45,47,48,54	•••	1	•••	•••	•••		
38,39,46,48,50,55,56/35,40,45,47,54	•••	•••	•••	•••	2	•••	
35,38,48,50,54,55,56/39,40,45,46,47	•••	•••	•••	•••	•••	1	
35,38,39,48,50,55,56/40,45,46,47,54	•••	•••	•••	•••	•••	3	
5,38,39,40,50,55,56/45,46,47,48,54	•••	4	•••	•••	•••	•••	
9,46,48,50,55,56/35,38,40,45,47,54	•••	1	•••	•••	•••	•••	
9,40,50,54,55,56/35,38,45,46,47,48		1			•••	•••	
8,39,48,50,55,56/35,40,45,46,47,54	•••	1	•••	•••	•••		
8,39,40,50,55,56/35,45,46,47,48,54		1		•••			
3,38,48,50,55,56/39,40,45,46,47,54			2				
5,38,39,50,55,56/40,45,46,47,48,54		1	1				
35,38,39,48,50,56/40,45,46,47,54,55	2			•••		3	
5,38,39,45,50,56/40,46,47,48,54,55		•••	1				
			2				
5,38,48,50,56/39,40,45,46,47,54,55	•••	•••	2	-••		•••	
Total no. of isolates	23	32	32	8	19	8	
Mean virulence capability <sup>a</sup>	2.9	3.3	2.8	2.6	2.6	5	

<sup>&</sup>lt;sup>a</sup> Mean virulence capability =  $\Sigma(a \times b)/c$ , where a = no. of isolates of a virulence combination, b = no. of ineffective host (Pc) genes in that combination, and c = total no. of isolates.

virulence characteristics were not greatly different except for some isolated regiongene variations. It is possible that these variations would be smoothed out over a longer survey period. However, the results also indicate a complex epidemiology for P. coronata var. avenae. In the milder regions, the fungus may overwinter on hosts susceptible to crown rust, creating localized epiphytotics. Also, the alternate host, Rhamnus cathartica L. (European buckthorn), is quite widely distributed and thus may modify localized distribution of virulence frequencies. Because there are no major geographic barriers in central Europe, long-term exchange of inoculum would be expected to occur.

The major variations in virulence were in the extreme southern regions. Although the data from southern Italy and Yugoslavia were somewhat limited, the results indicate common virulence frequencies between these regions. The crown rust isolates from Portugal differed substantially on genes Pc 38, 39. 50, and 56 (Table 3) as compared with those from Italy and Yugoslavia. This indicates that the sources of inoculum for these widely separate regions are different. There appears to be little inoculum exchange between southern and central Europe, as indicated by the virulence frequencies and the mean virulence capabilities.

The Pc genes used in this study are all derived from accessions of A. sterilis that originated from eastern and North African regions of the Mediterranean basin. A. sterilis also occurs in most regions of southern Europe, although the occurrence of Pc genes in this area is not yet known. The high levels of virulence of P. coronata var. avenae from southern Europe on the Pc-gene lines suggests that these populations of P. coronata var avenae have evolved in the presence of natural populations of A. sterilis that contain these genes. There may also be exchange of inoculum between southern Europe and the Middle East and North Africa.

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**Table 2.** Virulence combinations of isolates of *Puccinia coronata* var. avenae from Austria (A), Czechoslovakia (CS), Germany (D), Denmark (DK), Italy (I), Poland (P), Portugal (PL), and Switzerland (CH) on lines of *Avena sativa* containing known genes (*Pc*) for crown rust resistance in 1980

Virulence combination (effective/ineffective)	Number of isolates							
of host resistance $(Pc)$ genes	A	СН	CS	D	DK	I	P	PL
35,38,39,40,45,46,47,48,50,54,55,56,62,63/	1	3	3	12	1		•••	•••
38,39,40,45,46,47,48,50,54,55,56,62,63/35	•••	•••	2	3	•••	•••	2	•••
35,39,40,45,46,47,48,50,54,55,56,62,63/38 35,38,39,45,46,47,48,50,54,55,56,62,63/40	•••			1	~~	•••	•••	•••
35,38,39,40,46,47,48,50,54,55,56,62,63/45	1		•••	6 	7 3			
35,38,39,40,45,47,48,50,54,55,56,62,63/46			•••	1				
35,38,39,40,45,46,48,50,54,55,56,62,63/47	•••	•••	•••	1	•••	•••	•••	1
35,38,39,40,45,46,47,50,54,55,56,62,63/48	•••		•••	•••	1	•••	•••	•••
35,38,39,40,45,46,47,48,50,55,56,62,63/54 35,38,39,40,45,46,47,48,50,54,55,62,63/56		1 		• • • • • • • • • • • • • • • • • • • •		•••	•••	•••
35,38,39,40,45,46,47,48,50,54,55,56,63/62	•••	•••		2	1 		•••	
35,38,39,40,45,46,47,48,50,54,55,56,62/63	1	•••	•••	1				
38,39,40,46,47,48,50,54,55,56,62,63/35,45	•••	•••	•••	•••	•••	•••	1	•••
38,39,40,45,47,48,50,54,55,56,62,63/35,46 38,39,40,45,46,47,48,50,54,55,62,63/35,56	•••	•••	•••	•••	1	•••	•••	•••
38,39,40,45,46,47,48,50,54,55,56,62/35,63					2			•••
35,39,40,45,46,47,48,50,54,55,56,62/38,63			1			•••	1	
35,38,40,45,46,47,50,54,55,56,62,63/39,48	•••	•••	1		•••	•••		
35,38,39,46,47,48,50,54,55,56,62,63/40,45	•••	•••	•••	1	•••	•••	•••	•••
35,38,39,45,46,48,50,54,55,56,62,63/40,47 35,38,39,45,46,47,48,50,55,56,62,63/40,54	•••	1	•••	9	•••	•••	•••	•••
35,38,39,45,46,47,48,50,54,55,62,63/40,56			1			•••		
35,38,39,45,46,47,48,50,54,55,56,63/40,62		•••	•••	2				
35,38,39,40,46,48,50,54,55,56,62,63/45,47	•••	•••	•••		1			
35,38,39,40,45,46,48,50,54,55,56,63/47,62	•••	2	•••	•••	2	•••	•••	•••
35,38,39,40,45,46,47,48,50,55,56,62/54,63	•••	.•••	1	•••	•••	•••	•••	•••
35,38,39,40,45,46,47,48,50,54,55,62/56,63 39,40,45,46,47,50,54,55,56,62,63/35,38,48		•••	•••		1 1	•••	•••	•••
39,40,45,46,47,48,50,54,55,62,63/35,38,56	•••	•••			1			
39,40,45,46,47,48,50,54,55,56,62/35,38,63	3	•••	•••	1	2		1	
38,39,40,45,46,48,50,54,55,56,62/35,47,63		•••	1	•••	•••	•••		•••
35,39,45,46,47,48,50,54,55,56,62/38,40,63 35,38,39,46,48,50,54,55,56,62,63/40,45,47			1		•••	•••	•••	•••
35,38,39,45,46,48,50,55,56,62,63/40,47,54	1	3		2 1				
35,38,39,40,48,50,54,55,56,62,63/45,46,47								1
35,38,39,40,47,48,54,55,56,62,63/45,46,50	•••	1	•••	•••	•••	•••	•••	
35,38,39,40,46,47,50,54,55,56,62/45,48,63	1	•••	•••	•••	•••	•••	•••	•••
39,40,45,46,47,50,54,55,56,62/35,38,48,63 39,40,45,46,47,48,50,54,55,62/35,38,56,63				•••		•••	2	•••
38,39,45,46,47,48,50,54,55,62/35,40,56,63	•••	•••			5 		2	•••
35,38,39,46,48,50,54,55,62,63/40,45,47,56	•••	•••	•••	2				
35,38,39,45,48,50,55,56,62,63/40,46,47,54	•••	•••	•••	1	•••	•••	•••	•••
35,38,39,40,48,50,55,56,62,63/45,46,47,54 35,38,39,40,45,47,48,50,55,62/46,54,56,62	•••	1	•••	1	•••		•••	1
35,38,39,40,45,47,48,50,55,63/46,54,56,62 39,45,48,50,54,55,56,62,63/35,38,40,46,47	2	•••		•••		•••	•••	1
38,39,46,48,50,55,56,62,63/35,40,45,47,54		•••				1	•••	
35,39,40,47,48,54,55,56,62/38,45,46,50,63	•••	•••	•••	•••	1		•••	
35,38,39,48,50,55,56,62,63/40,45,46,47,54	•••	•••	•••	1	•••	1	•••	1
35,38,39,45,48,50,55,62,63/40,46,47,54,56 15,38,39,40,50,55,56,62,63/45,46,47,48,54	•••	•••	•••	•••	•••		•••	1
15,38,39,40,48,50,55,56,63/45,46,47,54,62		1				1	•••	
9,46,48,50,54,55,56,62/35,38,40,45,47,63			1					•••
8,46,48,50,55,56,62,63/35,39,40,45,47,54	•••	•••	•••	•••	•••	1	•••	
8,46,48,50,54,55,62,63/35,39,40,45,47,56	•••	•••	•••	•••	•••	1	•••	•••
8,39,48,50,55,56,62,63/35,40,45,46,47,54 8,39,45,48,50,55,56,63/35,40,46,47,54,62	•••	•••	•••	•••	•••	5	•••	•••
8,39,40,50,55,56,62,63/35,45,46,47,48,54				•••		_	•••	1
8,39,40,45,48,50,55,63/35,46,47,54,56,62	•••	•••		•••		-		1
5,39,40,45,50,54,55,63/38,46,47,48,56,62	•••	•••		•••	•••			î
5,39,40,45,48,50,55,63/38,46,47,54,56,62 5,38,30,46,48,55,63/38,46,47,50,54,56	•••	•••	•••	•••	•••		•••	1
5,38,39,46,48,55,62,63/40,45,47,50,54,56 5,38,39,45,48,50,55,63/40,46,47,54,56,62	•••			1	•••		•••	
5,38,39,40,48,50,55,63/45,46,47,54,56,62								1
5,38,39,40,46,48,55,63/45,47,50,54,56,62	•••							1
9,40,48,50,55,62,63/35,38,45,46,47,54,56	•••		•••	•••	•••			1
, , , , , , , , , , , , , , , , , , , ,			2	•••				
8,46,50,55,56,62,63/35,39,40,45,47,48,54	•••	•••			•••	••• •	••	•••
8,46,50,55,56,62,63/35,39,40,45,47,48,54 8,39,48,50,55,62,63/35,40,45,46,47,54,56	•••	•••	•••	•••			••	2
8,46,50,55,56,62,63/35,39,40,45,47,48,54							••	

(continued on next page)

Table 2 (continued from preceding page)

Virulence combination (effective/ineffective)		Number of isolates								
of host resistance $(Pc)$ genes	A	СН	CS	D	DK	I	P	PL		
35,39,40,50,55,56,63/38,45,46,47,48,54,62								1		
35,38,50,55,56,62,63/39,40,45,46,47,48,54		•••	•••	3		•••		•••		
35,38,39,48,55,62,63/40,45,46,47,50,54,56		•••	•••	•••	•••	•••		1		
35,38,39,45,48,55,63/40,46,47,50,54,56,62		•••		•••		•••		1		
35,39,46,48,55,63/38,40,45,47,50,54,56,62		•••	•••		•••	•••		7		
Total no. of isolates		10	13	23	49	32	9 10	29		
Mean virulence capability <sup>a</sup>		2.7	2.2	3.4	1.6	2.0	5.7 2.9	6.3		

<sup>\*</sup>Mean virulence capability =  $\Sigma(a \times b)/c$ , where a = no. of isolates of a virulence combination, b = no. of ineffective host (Pc) genes in that combination, and c = total no. of isolates.

**Table 3.** Percentage of isolates of *Puccinia coronata* var. avenae with virulence on lines of Avena sativa with specific genes (Pc) for crown rust resistance

Host resistance (Pc) gene		Country or region <sup>a</sup>									
	A	СН	CS	D	DK	I	P	PL	SU/L	SU	YU
Avirulentb	2.5	21.4	5.8	23.0	3.4	0.0	8.9	0.0	0.0	5.3	0.0
Pc 35°	42.5	0.0	40.6	7.6	41.4	77.8	57.8	17.2	38.5	89.5	14.3
Pc 38°	35.0	0.0	27.5	3.8	34.5	0.0	35.6	48.3	69.2	26.3	0.0
Pc 39°	0.0	0.0	8.6	0.0	0.0	22.2	8.9	0.0	0.0	0.0	14.2
Pc 40°	40.0	35.7	23.2	50.0	31.0	77.8	31.1	62.1	30.8	42.1	100.0
Pc 45°	30.0	42.8	33.3	17.3	13.8	100.0	26.7	65.5	0.0	31.6	100.0
Pc 46°	22.5	21.4	23.2	7.7	6.9	66.7	24.4	65.5	0.0	0.0	85.7
Pc 47°	32.5	35.7	27.5	38.5	0.0	100.0	20.0	96.6	0.0	31.6	100.0
Pc 48°	2.5	0.0	26.1	0.0	6.9	22.2	8.9	3.4	0.0	0.0	0.0
Pc 50°	0.0	7.1	0.0	1.9	3.4	0.0	0.0	37.9	23.0	0.0	0.0
Pc 54°	20.0	21.4	28.9	9.6	0.0	88.9	24.4	89.7	0.0	15.8	71.4
Pc 55°	5.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	7.7	0.0	25.6
Pc 56°	0.0	0.0	5.8	5.8	20.7	11.1	20.7	75.9	38.5	15.8	0.0
Pc 58 <sup>d</sup>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pc 59 <sup>d</sup>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pc 60 <sup>d</sup>		0.0		5.8	0.0	66.7		10.3			
Pc 61 <sup>d</sup>		0.0		7.7	0.0	66.7	•••	10.3			
Pc 62 <sup>d</sup>	0.0	28.6	0.0	11.5	0.0	0.0	0.0	62.1			•••
Pc 63 <sup>d</sup>	50.0	0.0	34.8	3.8	31.0	0.0	70.0	0.0	•••		

<sup>&</sup>lt;sup>a</sup> Austria (A), Czechoslovakia (CS), Fed. Rep. Germany (D), Denmark (DK), Italy (I), Poland (P), Portugal (PL), Soviet Union/Lithuania (SU/L), Soviet Union/northwestern (SU), Switzerland (CH), Yugoslavia (YU).

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<sup>&</sup>lt;sup>b</sup>Refers to percentage of isolates avirulent on all of the *Pc*-gene lines tested.

<sup>&</sup>lt;sup>c</sup>Data for A and CS are from 1977–1980; P from 1977, 1978, and 1980; SU/L and YU from 1979; SU from 1978; D, DK, I, PL, and CH from 1980.

<sup>&</sup>lt;sup>d</sup>Data are from 1980.