New Pathogenic Variability in Uromyces appendiculatus in North America

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ABSTRACT

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From 43 field collections of urediniospores of *Uromyces appendiculatus* obtained from nine states, Puerto Rico, and the Dominican Republic from 1983 to 1987, new virulence combinations were identified in 13 single-uredinium isolates, described here as races 58–70. Isolates of 11 previously described races were obtained. Two of the new races have broader virulence on the cultivars used to differentiate races than the previously described North American races. Race 67 is the first to produce moderate-size uredinia on a previously resistant selection of the bean cultivar Compuesto Negro Chimaltenango. Others of these newly described races are the first to contain certain important combinations of virulence on some of the more resistant differential cultivars. The implications of these results are discussed in relation to the development of comprehensive and stable rust resistance in the common bean.

Additional keywords: bean rust, Phaseolus vulgaris

Pathogenic variability in Uromyces appendiculatus (Pers. ex Pers.) Unger var. appendiculatus (syn. U. phaseoli (Reben) Wint.), the rust pathogen of common bean, Phaseolus vulgaris L., is extensive and commonly encountered (26). In the United States, 55 pathogenic races (8,11,14,22,26,28) and additional variability (10) have been reported over the past 48 yr. In addition, about 150 races have been identified in Latin America (1,3,4,6,7,12,17,27), Australia (2), and Africa (15). To standardize the identification of this variability and enhance the usefulness of such identifications, a standard set of 19 differential cultivars and a standard grading scale with defined reaction grades (infection types) were adopted at an international bean rust workshop in Puerto Rico in 1983 (24). These differential cultivars were representative of available resistant germ plasm and resistance genes.

Resistance to rust in bean cultivars has been effective in reducing losses from *U. appendiculatus* in spite of this pathogenic variability. Cultivars such as Aurora

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small white, C-20 and Fleetwood navies, and Olathe pinto have generally remained resistant in their areas of cultivation for several to many years (J. R. Stavely and J. R. Steadman, *unpublished*). However, the identification of U.S. races of the pathogen virulent on these and other such cultivars indicates their vulnerability (22)

Obtaining stable rust resistance in beans may necessitate the pyramiding of broadly effective specific resistance genes into traditional cultivars, the development of multiline cultivars, or the identification and use of some less specific kind of resistance (15,21-23). The availability of a wide range of pathogenic variability facilitates the identification of resistance mechanisms and resistance genes distinct from those already identified and enhances opportunities for pyramiding. By obtaining and using a race virulent on a source of resistance broadly effective against other races, one can identify and select for additional resistance. A wide range of pathogenic variability is also useful in determining if putatively non-racespecific or "horizontal" resistances are truly nonspecific.

The objective of this study was to identify races of *U. appendiculatus* having new patterns of virulence on the most broadly resistant bean germ plasm available, as represented in the differential cultivars.

MATERIALS AND METHODS

Urediniospore collections and singleuredinium isolations. The urediniospore collections containing the new races described here were obtained by previously described methods (20,22) from four distinct areas: a dry bean production area in Scotts Bluff County, Nebraska; a snap bean production area in Dade County, Florida: Isabella, Puerto Rico; and a large-seeded dry bean production area in Higuey, in the eastern Dominican Republic. The Puerto Rican collection was from an experimental plot of two dry bean breeding lines, L-226 and B-190, which have the same broad resistance to most races as Mexico 309 (22). The Dominican collection was from Florida 72, another line having resistance to numerous races. The Nebraska collection was obtained late in the growing season from Great Northern Valley. Twelve collections were obtained from various bush and pole cultivars in the area of Homestead, Florida. Preliminary work was done on the Nebraska and Dominican collections by Steadman et al (27) and Ramirez Mejia (16) at the University of Nebraska, which aided in the selection of two specific collections that appeared to have a mixture of races likely to include a race or races of particular significance. Inoculations with the Puerto Rican and Dominican collections were done in the USDA containment greenhouses at Frederick, Maryland. Definitive studies with the Florida and Nebraska collections as well as with other field collections, obtained from Colorado, Maryland, Michigan, New Jersey, Tennessee, Virginia, and Wisconsin, were conducted at Beltsville, Maryland.

Field collections of urediniospores were used to inoculate the 19 standard differential cultivars (22,24,26). The emphasis in making single-uredinium isolations was placed on single, isolated, moderate to large uredinia (0.5 mm in diameter or larger) from the cultivars susceptible to the fewest of the previously described U.S. races (22). However, with the collections from Nebraska and snap beans, identification of as much variability as possible was desired, so uredinia were also isolated from some of the more susceptible cultivars (9,22). The first increase from each uredinium produced sufficient spores to inoculate the standard differential cultivars as well as multiple plants of a susceptible cultivar, to increase urediniospores for additional inoculations. Care was always taken to inoculate seedlings that were produced under rust-free conditions. Inoculated plants were kept isolated during inoculation and incubation to avoid chance infection by any other spores of the fungus.

Bean cultivars, plant propagation, and inoculation method. The 19 standard differential cultivars were used to determine the purity and describe the virulence of each isolate. Seed of these 19 was selectively increased from single plants and tested at Beltsville for at least three successive generations, so that each cultivar was homozygous for reaction to all available races of *U. appendiculatus* (22). Appropriate differential cultivars were added to those in the standard set of 19, to compare each isolate with races previously reported in Australia (2), Brazil (1), and Mexico (7). Seed of the Australian differentials was obtained from B. J. Ballantyne (2). Seed of the Brazilian and Mexican differentials was obtained from the International Bean Rust Nursery and was distributed by the Centro Internacional de Agricultura Tropical, Cali, Colombia. Five seeds of a single cultivar were germinated in each pot, in the soil mixture and under the greenhouse conditions described earlier

Unifoliolate leaves were uniformly spray-inoculated on both surfaces when they were 35–65% expanded, which was usually 6–8 days after seeding, depending upon the season. As many as eight single-uredinial isolates were tested on as many as 35 cultivars per trial. Inoculum preparation was as previously described (20), with the spore concentration adjusted to 16,000 or 20,000 urediniospores per milliliter of 0.1% Tween 20 in tap water. All tests with suspected new races obtained from single-uredinium

isolates were repeated at least four times, with inoculum at the higher concentration in at least one test. The higher concentration is desirable for detecting necrotic reactions, and the lower for obtaining maximal uredinium size. The sprayinoculated plants were allowed to dry and placed in a Percival Model I-35 DL dew chamber for 16 hr, from afternoon to morning, at about 19 C with dew deposition. Upon subsequent drying of the leaves, the plants were moved to a greenhouse having thermostatically controlled heating and cooling to give a temperature range of 22-28 C. All tests were conducted between late February and early May.

Rust ratings. Rust infection types and intensities (15,22,24) were recorded for both leaf surfaces of each cultivar on the 14th day after inoculation. Leaves were tapped to remove excessive urediniospores before the infection type was rated. Printed cards having dots approximately 0.3, 0.5, and 0.8 mm in diameter (22,24), printed sheets having examples of six uredinium intensities, and a hand lens aided in the assignment of appropriate values. The occurrence of some variation in infection type with environmental variation is well documented (11,20,23), so only types obtained in at least two identical definitive tests are reported here.

RESULTS

Newly identified virulences, assignment of race numbers, origins, and observations on variability. On the

standard set of differential cultivars (22,24), 13 virulence patterns that differed from those previously reported in the United States (8,10,11,14,22,28) were identified for *U. appendiculatus* (Tables 1 and 2). These pathotypes have been assigned race numbers 58-70, in the order in which they were obtained. The reported reactions of appropriate differential cultivars distinguished races 1-37 (8,11,14,28) from each of the new races. Races 58-70 were similarly distinguished from the more recently reported races 38-57 (22). The closest similarity between previously reported races and these new races occurred between races 41 and 60 and between races 48 and 62. However, when repeated parallel inoculations with these two pairs of races were conducted, the differential reactions of Kentucky Wonder (KW) 765, Mexico 235, Actopan × Sanilac Selection 37 ($A \times S$ 37), and Compuesto Negro Chimaltenango (CNC) consistently separated races 41 and 60, and the differential reactions of Brown Beauty and KW 765 separated races 48 and 62.

Races 58-61, 63-67, 69, and 70 were each obtained from only one single-uredinium isolate from one urediniospore collection. The collection from Nebraska was highly variable, containing races 59-61, 63, and 64 as well as the previously described race 53 (22). Race 59 constituted about 60% of the mixture. The Dominican collection also produced variable reactions, indicating the presence of more than one pathotype. Race 58 was the minor component and race 62 the major

Table 1. Infection types of differential bean cultivars in reaction to races 58-64 of Uromyces appendiculatus

Differential cultivar ^a	Pathogenic races ^{b,c}								
	58 (DR)	59 (NE)	60 (NE)	61 (NE)	62 (DR)	63 (NE)	64 (NE)		
a. U.S. 3	5,6	2++,2+d	5,6	6,5/5,6	5,4,6	4,5/2+,3	2++,2+d		
b. CSW 643	5,4	3,2	3	2	3,4	5,4,6/4,5,6	4,5,6/5,6,4		
c. Pinto 650	5,6/6,5	6,5/5,6	6,5/5,6	5,6,4	5,6,4	5,6,4	5,4,6		
d. KW 765	4,5	2,3	3,2	3	3	4,3,5/3,2,4	4,3,5/3,2		
e. KW 780	5,6	6,5	6,5	5,6	2+,2++d	2+,2++d	2+,2++4		
f. KW 814	3,2/2	4,5,3	4,5	3,4	4,5	3,2/2	3,2/2		
g. Golden Gate Wax	4,5	2	$2+,2^{d}$	2	4,5	2	2		
h. Early Gallatin	4/4,5	4,5	4/4,5	4,5	2+,2	2+,2	2+,2		
i. Redlands Pioneer	4/4,5	2,3/3	4,5	2,3/3	4/4,5	2+,2	4/4,5		
i. Ecuador 299	3,2/3,4	2	2	2 '	3	5,6,4/6,5	5,6/6,5		
k. Mexico 235	3,2/3	2	2	2	3,2/3	5,6/6,5	3/3,4		
l. Mexico 309	5,4/5,6	3,2/3	3,2/3	3,2/3	3,2/3	3,2/3	3,2/3		
m. Brown Beauty	4,3,5	4,3,5	4,5	4,5	2+,2,3	2+,2	2+,2		
n. Olathe	4,5	2	2,2+	2	3,4	2	2		
o. $A \times S$ 37	2,3/3	2,3/3	2,3/3	2,3/3	5,4/5,6,4	2,2+/2,2+,3	2,2+/2,2+,3		
p. NEP-2	5,4/5,6	2,2+	2,2+	2,2+	5,4,6	2,3,2+	3,2/3		
q. Aurora	5,6,4	2,2+	2,2+	2,2+	6,5	5,6,4	5,6,4		
r. 51051	3,2/3,4	2,2+	2,2+	2,2+	3	1	3,2		
s. CNC	2	3,2	3,2	3	2	3,4	3,4		

^aU.S. = United States; CSW = California Small White; KW = Kentucky Wonder; A × S 37 = Actopan × Sanilac Selection 37; CNC = Compuesto Negro Chimaltenango.

^bPlaces of origin are given in parentheses: DR = Dominican Republic; NE = Nebraska.

cReaction grades: 1 = immune; 2 = necrotic spots without sporulation and less than 0.3 mm in diameter; 2+ = necrotic spots 0.3-1 mm in diameter; 2++ = necrotic spots 1-3 mm in diameter; 3 = uredinia less than 0.3 mm in diameter; 4 = uredinia 0.3-0.5 mm in diameter; 5 = uredinia 0.5-0.8 mm in diameter; and 6 = uredinia larger than 0.8 mm in diameter. Where a slash is given, numbers to the left of the slash are for the adaxial leaf surface, and numbers to the right are for the abaxial leaf surface. Where several figures are given, they are listed in order of predominance, from most to least predominant.

dSome of the larger necrotic spots contained a small uredinium.

component in this collection. Race 62 was subsequently identified in a 1987 collection from Florida and a 1983 collection from Puerto Rico. Race 65 was the only race in the 1984 Puerto Rican collection from L-226 and B-190. Races 66-70 were obtained from collections made in Dade County, Florida, in 1984, 1985, and 1987. Race 68 was isolated once in 1985 and twice in 1987.

Variability in *U. appendiculatus* from Dade County and adjacent southern Florida counties was as great as that in any other place so far investigated (2-4,7,8,10-12,15-17,22,26). Seventeen of the races described here or in earlier reports (14,22) were found there. The most variable single-field collections of urediniospores from there came from the climbing snap bean cultivars McCaslan and Princeton. The collection from Princeton contained races 52–54 and 68, and the one from McCaslan contained these four and races 62 and 70. Although races 66, 67, and 69 were not present in either of these highly variable collections, they were obtained from other collections from McCaslan or from small experimental plantings of the dry bean cultivar Pinto 111. Abundant teliospores occurred on older leaves of McCaslan. Greenhouse tests at Beltsville showed McCaslan to be susceptible to all available races except 38 and 39, to which it reacts with a necrotic, grade 2++ infection type.

Comparison with previously reported races from other countries. The closest similarity between any race reported here and those previously described from

other countries was between race 62 and Mexican race 17 (7). On all of the Mexican differential cultivars except Mexico 12, race 62 produced reactions like those reported for Mexican race 17. Our accession of Mexico 12 was mixed, so that some plants had a 2,3/2,2+,3reaction and others had a 4,5/5,4 reaction to race 62. Mexico 12 was fully susceptible to Mexican race 17 (7). None of races 58-70 produced the same combination of reactions on the appropriate sets of differential cultivars as any of the Australian (2), Jamaican (17), Tanzanian (15), or Brazilian (1,3,4,12)

Previously described U.S. races isolated. Ten of the races described in 1984 (22) and one described earlier (11) were identified in the 43 different field collections of urediniospores evaluated from 1983 to 1987. Race 38 was the sole or predominant race in all collections from bush snap beans. It was found in 22 collections from Florida, Maryland, New Jersey, Tennessee, Virginia, and Wisconsin. This is the first report of its occurrence in Wisconsin. Races 39, 44. and 48 were each isolated from different Florida collections, and race 42 was obtained from a New Jersey collection. Among previously reported races virulent on Olathe, races 52, 53, 54, and 56 were present in four, three, four, and three, respectively, of the Florida collections analyzed from 1983 to 1987. Race 54 was the first virulent race ever isolated from Olathe in Colorado, where it was collected in 1986. A collection obtained

from Michigan in 1985 contained race 40 (22) and Harter and Zaumeyer's race 4 (11).

DISCUSSION

Most of the races identified here and earlier (15,20) are distinguished by widely different host reactions in one or more differential cultivars. We rarely used differences of lesser degree, as in distinguishing races 41 and 60. When repeated parallel, separate inoculations with a new single-uredinium isolate and a questioned identical race consistently yielded a nonsporulating, grade 2 reaction in one and minute, grade 3 uredinia in the other, the difference was considered sufficient to differentiate the isolates as unique races. Distinct host genes have been shown to control these different kinds of reactions (2,5,21,25). Environmental factors have long been recognized to have some effect on the reactions of beans to this pathogen (11,22,26), and with the arbitrary definitions of infection types based on the size of uredinia in host reactions (24), a 4,3 reaction in December can become a 4,5 reaction in June. However, there are limits on the degree of this kind of variation as long as environmental extremes are avoided and leaf age (18,19) and infection intensity (11,20,26) are controlled. Widely different infection types on a leaf, such as a 2 or 3 being present with a 6, occur only when two or more races are present. Although this is frequently encountered in field urediniospore collections containing more than

Table 2. Infection types of differential bean cultivars in reaction to races 65-70 of Uromyces appendiculatus

Differential	Pathogenic races ^{b,c}									
cultivar ^a	65 (PR)	66 (FL)	67 (FL)	68 (FL)	69 (FL)	70 (FL)				
a. U.S. 3	5,6/4,5,6	4,5,3/2+,3	5,4,6	5,6/5,6,4	5,6/5,4,6	5,6/5,6,4				
b. CSW 643	3,2/3,4	5,6,4/5,4,6	3,2/3	3,2/3,4	3,4	5,6/5,4,6				
c. Pinto 650	6,5/5,6	5,6/5,4,6	5,6,4	5,6,4	6,5/5,4,6	6,5/5,4,6				
d. KW 765	3,2/3,4	4,5,3/2+	3,2/3	4,5/5,4	4,5/5,4	4,5				
e. KW 780	2+,2++d	2+,2++d	5,4,6	5,6	2+,2++d	2+,2++				
f. KW 814	6,5/5,4,6	3,2/2,3	4,5	4,5	4,5	4,5				
g. Golden Gate Wax	6,5/5,6,4	2	4,5	4/4,3	4,5/3,4	4,5/3,4				
h. Early Gallatin	2+,2	2+,2	4/4,5	4,5	2+,2	2+,2				
i. Redlands Pioneer	5,6,4	4,5	4/4,5	3/3,4	4,5	4/4,5				
j. Ecuador 299	3,2/3,2,4	5,6/6,5	3,2/3,4	2	2	2, .,5				
k. Mexico 235	3,2/2,3	5,6/6,5	2 '	2	$\overline{2}$	2				
l. Mexico 309	6,5,4	3,2/3	4,5/5,4,6	3,2/3	$\frac{-}{3,2/3}$	$\frac{1}{3}$,2/3				
n. Brown Beauty	2+,2	2+,2	4/4,5	4/4,5	2+,2,3	2+,2				
n. Olathe	3,2/3,4	2	3,2/3	4,5/4,3	4,5/3,4	5,6,4/4,3				
o. $A \times S$ 37	5,6,4/5,4,6	3,2/3	5,4/5,6,4	2,3/3	2,3	2,2+,3				
o. NEP-2	5,4,6	3,2/3	4,5/5,4,6	2,2+	2,2+	2,2+				
ą. Aurora	5,4,6	5,4/5,6,4	4,5/5,6,4	2,2+	2,2+	2,2+				
r. 51051	4,5/5,4,6	3	4,5/5,4,6	2,2+	2,2+	2,2+				
s. CNC	3,4	3,2/3	4,3/4,5,3	3,2/3	2,3/3,2	$\frac{2,2}{3,2/3}$				

^aU.S. = United States; CSW = California Small White; KW = Kentucky Wonder; A × S 37 = Actopan × Sanilac Selection 37, CNC = Compuesto Negro Chimaltenango.

^bPlaces of origin are given in parentheses: FL = Florida; PR = Puerto Rico.

Reaction grades: 1 = immune; 2 = necrotic spots without sporulation and less than 0.3 mm in diameter; 2+ = necrotic spots 0.3-1 mm in diameter; 2++ = necrotic spots 1-3 mm in diameter; 3 = uredinia less than 0.3 mm in diameter; 4 = uredinia 0.3-0.5 mm in diameter; 5 = uredinia 0.5-0.8 mm in diameter; and 6 = urédinia larger than 0.8 mm in diameter. Where a slash is given, numbers to the left of the slash are for the adaxial leaf surface, and numbers to the right are for the abaxial leaf surface. Where several figures are given, they are listed in order of predominance, from most to least predominant.

dSome of the larger necrotic spots contained a small uredinium.

one race, it has not been encountered with pure isolates, either here (Tables 1 and 2) or elsewhere (1-4,7,8,11,12,15, 17,22,26).

The highly variable pathogenicity of U. appendiculatus has been recognized for many years (11,26). A single field collection often contains several to many races, as is reported here for collections from western Nebraska and southern Florida and was previously reported for collections from North Dakota (22), Tanzania (15), Brazil (3,4,12), and Australia (2). Geographic region and climate appear to have little relation to the occurrence of this variability. The completion of the life cycle to permit genetic recombination has been shown to be a major factor contributing to high variability in rust fungi (9), which seems to suggest that pycnial and aecial stages probably occur in all of the places mentioned above, even though they have been identified only in northern latitudes so far (26). Cultivar susceptibility to a wide range of races may play a role in this variability by permitting the occurrence of multiple pathogen virulence genes. Most U.S. bush snap bean cultivars are identical or nearly identical to the differential cultivar Early Gallatin in their reactions to the 13 races described here and the 20 described a few years ago (22; J. R. Stavely, unpublished). They are moderately susceptible, developing intermediate-size uredinia and telia, or hypersensitively resistant, having a nonsporulating, necrotic reaction, to races 40–70, and they are fully susceptible only to races 38 and 39, which do not produce teliospores. Race 38 is the principal and often the sole race on snap beans. On the other hand, Great Northern Valley, McCaslan, and Princeton have large-uredinium susceptibility to many races that produce abundant teliospores on them (J. R. Stavely, unpublished).

Among the races described here are several having important previously unreported virulence combinations or characteristics. Race 58 is the first described North American race of U. appendiculatus to produce moderately to highly susceptible reactions in Early Gallatin, Mexico 309, NEP-2, and Aurora as well as in Olathe. Race 67 is the first race to which CNC has any degree of susceptibility (6,15,22). This cultivar has immune, necrotic, or small-uredinium reactions to all other races. Races 58 and 67, which produced moderate to large uredinia on 13 and 14 of the 19 differential cultivars, respectively, have broader virulence than any previously described North American races. Races 63 and 66 are virulent on Mexico 235 and Ecuador 299, which are susceptible to only two of the races described in 1984 (22). Race 64 is the first race to which Mexico 235 and Ecuador 299 have widely different reactions. Races 64 and 66 are

the first with moderate to high virulence on both Ecuador 299 and Redlands Pioneer. Race 66 is the first with virulence on both Mexico 235 and Redlands Pioneer. Among the more broadly resistant of the remaining differential cultivars, 51051, Mexico 309, $A \times S$ 37, NEP-2, Olathe, California Small White 643, and Aurora were moderately or more susceptible, respectively, to two, three, three, four, five, and seven of the 13 new races. The pairs of differential cultivars for which combined moderate to highly susceptible reactions to a single race have not yet been identified anywhere have now been reduced to CNC and Mexico 235, Ecuador 299, Olathe, California Small White 643, or KW 765; Mexico 235 or Ecuador 299 and Early Gallatin, KW 780, Golden Gate Wax, Olathe, or Brown Beauty; 51051 and Olathe; and Olathe and $A \times S$ 37 (15,22).

The pathogenic variability described here and earlier (15,22) is sufficient to indicate genetic similarities and differences in rust resistance of the standard differential cultivars (21,23). Two of the cultivars, Ecuador 299 and Mexico 235, react identically to most races. Race 64 produces the only major differential reaction in them. Five of the differential cultivars, Aurora, Ecuador 299, Mexico 235, NEP-2, and 51051, with only three exceptions out of 480 possible combinations of race, host reaction, and host cultivar, develop small (grade 2 or grade 2,2+) necrotic spots or flecks in response to races 40-42, 52-57, 59-61, and 68-70 and Tanzanian races T-1-T-7. This strongly suggests that these five cultivars contain the same gene or gene complex conditioning this reaction to these races. This broadly effective gene is probably the same as Ballantyne's Ur-3 resistance gene, which conditions this same response to all 22 of her Australian races (2). Recent genetic evidence confirmed a single gene in Aurora controls this necrotic reaction to at least six races (13). If a complex locus is involved, as the three exceptions might suggest, the component genes or alleles must be very tightly linked. A different gene or locus conditioning a necrotic reaction is indicated by the reactions to races 38-70 and T-1-T-9 of KW 780, Early Gallatin, and most bush green and wax snap bean cultivars currently popular in the United States. This second hypersensitivity gene conditions larger necrotic spots (grade 2+,2 or grade 2+,2++) to races 40, 44, 48-51, 54, 62-66, 69, and 70, which are easily distinguishable from the necrotic reaction of Aurora to other races. This second, common gene is probably the same as Christ and Groth's Up-2 gene (5). Olathe and one of its reported parents, Golden Gate Wax (D. R. Wood, personal communication), appear to contain one or two genes in common that condition a grade 2, grade 2,2+, or grade

2+,2 reaction to races 40, 41, 43, 44, 47, 51, 60, 61, 63, 64, and 66. Mexico 309 contains closely linked single dominant genes, one per race, that condition its tiny-uredinium resistance to many of the races for which it has this reaction (21), and CNC and Mexico 235 apparently contain this same complex in addition to other monogenic resistance (23,25,26).

Most of the new races identified here appear to be of rare occurrence, because they have only been found once. However, they will be valuable in testing hybrid host populations to permit the detection and efficient combination of complementary resistance genes. The availability of races virulent on cultivars containing resistance genes or gene complexes effective against most races permits the transfer of these resistances to commercial cultivars and the inclusion of resistance to the races for which they are not effective. With sufficient knowledge of genetic relationships, adequate availability of races controlled and not controlled by such genes, and the use of multiple-race inoculation (20), it is possible to develop germ plasm lines and cultivars resistant to all available races, with more than a single gene for resistance to specific races. For such a gene-pyramiding scheme, broad representation of the range of pathogenic variability is essential. Continued monitoring of pathogen virulence and broader measurement of virulence frequencies are needed to improve the measurement of relative stability potentials of various components and combinations in resistance-gene-pyramiding schemes.

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