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Physiologic Specialization of *Puccinia recondita* f. sp. *tritici* in Nebraska During 1995 and 1996

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ABSTRACT

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Field samples of *Puccinia recondita* f. sp. *tritici*, collected from four wheat-growing regions in Nebraska in 1995 and from three in 1996, were characterized for virulence. Twenty virulence phenotypes were identified in 1995 and 18 in 1996. Virulence phenotypes MBR-10,18 (virulent on *Lr* genes, 1, 3, 3ka, 10, 11, 18, and 30) and MDR-10,18 (virulent on *Lr* genes 1, 3, 3ka, 10, 11, 18, 24, and 30) were the most prevalent, with each phenotype comprising 21.6% of the isolates characterized in 1995. Of the 1995 isolates, 24% were virulent on 10 or more host genes. No virulence to *Lr16* and *Lr17* was detected. In 1996, virulence phenotype MBR-10,18 was the most prevalent and comprised 20.5% of the isolates characterized. Of the 1996 isolates, 33% were virulent on 10 or more host genes. All isolates in both years were virulent on *Lr1, Lr3*, and *Lr10*. New virulence phenotypes were detected in 1996 that were not detected in 1995. In 1996, virulence was more frequent on *Lr2a, Lr16*, and *Lr17* and less frequent on *Lr3ka, Lr18, Lr24, Lr26*, and *Lr30*. The number of isolates virulent on *Lr24* and *Lr26* has decreased from 83 and 53%, respectively, in 1992, to 34 and 1%, respectively, in 1996.

Additional key words: near-isogenic lines, wheat leaf rust

Leaf rust of wheat (*Triticum aestivum* L.), incited by *Puccinia recondita* ex Desm. f. sp. *tritici* Eriks, is one of the most important wheat diseases worldwide. Certain wheat-producing countries (1,4,6,15) have conducted leaf rust monitoring programs to monitor physiologic specialization of this pathogen. Physiologic specialization of *P. recondita* was first reported by Mains and Jackson (8,9). Initially, they used the wheats Kanred and Malakof to separate *P. recondita* isolates, and then later used a differential series of 11 wheat cultivars to describe physiological races. The present nomenclature system in North America uses a series of 12 near-isogenic lines grouped into three sets of four differentials (7).

Based on a North American system of nomenclature described by Long and Kolmer (7), virulence within the natural leaf rust population is monitored through annual surveys in the United States (7) and Canada (4). In the Great Plains and in the Pacific Northwest, where leaf rust can be a potential threat to wheat production, virulence of *P. recondita* has been monitored through periodic surveys in North Dakota (16), Nebraska (17), Minnesota (12), Texas (10), and in eastern Washington and Oregon (14). These survey data are used to estimate the relative prevalence and distribution of pathotypes, to monitor the origin and spread of new virulence phenotypes, and to detect shifts toward virulence to resistance used in commercial cultivars.

In the Great Plains, virulence frequencies to specific host genes usually reflect the frequency with which those genes are used in commercial cultivars. Kolmer (2) reported that the virulence frequencies to *Lr1, Lr2a*, and *Lr2c* in the prairie provinces of Canada increased with the increased incorporation of these genes into commercial wheat cultivars grown in North Dakota, and that virulence phenotypes of *P. recondita* in Manitoba and Saskatchewan often change due to the effects of host selection (2). Kolmer and Liu (5) attributed the presence of *P. recondita* phenotypes virulent to *Lr16* in 1995 in Manitoba and Saskatchewan to the use of this gene in winter wheats in the prairie states of the United States. McVey and Long (13) postulated that the cultivars Redland and Arapahoe contain *Lr16*. In 1995, these cultivars accounted for approximately 38% of the total Nebraska hard red winter wheat acreage.

Resistance genes *Lr24* and *Lr26* became ineffective because of the shift of *P. recondita* phenotypes to virulence to *Lr24* and *Lr26* (2). The use of these 2 genes in commercial cultivars has declined in the last 5 years. For example, the Nebraska acreage of the cultivar Siouxland, which contains *Lr24* and *Lr26*, declined from 21% in 1988 to 4% in 1996.

The objectives of this study were to survey virulence of *P. recondita* in 1995 and 1996 in Nebraska and to identify new virulence phenotypes that may have developed since the 1992 and 1993 surveys.

MATERIALS AND METHODS

Collections of *P. recondita* were obtained in May and June of 1995 and 1996. Wheat growth stages for the collections ranged from growth stage 8 (ligule of last leaf just visible) to 11.1 (milky ripe) on the Feekes scale. As in previous years, surveys were conducted in four wheat-growing regions in Nebraska (panhandle, west-central, central, and east) in 1995. In 1996, uredinial collections were made from the west-central, central, and eastern wheat-growing regions. Collections were made approximately every 32 km or at the first field thereafter. The total number of samples collected varied in each region, and ranged from 15 in the panhandle to 44 in the east in 1995, and from 36 in the west-central to 69 in the east in 1996. Leaf rust was not found in the Nebraska panhandle in 1996; therefore, no uredinial collections were made from that region that year. The four regions differ somewhat in environmental characteristics and planting time, and to a lesser extent in cultivars grown. Average annual precipitation varies from 76 cm in the southeast to 38 cm in the panhandle. In both years the predominant cultivars in Nebraska were Arapahoe, Centura, AgriPro Thunderbird, Karl/Karl 92, Buckskin, Siouxland, AgriPro Abilene, Vista, and Redland.

A collection consisted of leaves bearing uredinia from each of 5 to 10 plants per field. Fields were sampled by randomly selecting plants at approximately 10-m intervals. Uredinia-bearing leaves were placed in glycine bags and stored in a cooler on ice until transported to the laboratory in the Department of Plant Pathology, University of Nebraska-Lincoln. In

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the laboratory, the leaves were transferred to plastic bags and stored at 3°C for 1 to 5 weeks. Each collection was then increased on 7- to 8-day-old seedlings of Thatcher (CI 10003). Inoculated plants were set in a dew chamber at 100% relative humidity at 20°C for an 18- to 24-h dark period. The plants were then placed at 20 to 25°C in a greenhouse in which natural daylight was supplemented with 400-W metal halide lights to provide a 14-h photoperiod.

Leaves were trimmed 10 to 12 days after inoculation, so that only one pustule remained on each plant. Urediniospores from single pustules were removed with a spatula and transferred to a microscope slide containing one drop of Tween 20. Hereafter, the use of uredinial isolate refers to a single-pustuled uredinial isolate. After the spores were mixed with the Tween 20, the slide was wiped onto the leaves of Thatcher to increase each uredinial isolate. The uredinial isolates were increased through one uredinial generation before inoculating the set of differentials. During this increase, the inoculated Thatcher plants were isolated in the greenhouse to prevent mixture of uredinial isolates. After 10 to 12 days, urediniospores were collected with a cyclone spore collector into a size-00 gelatin capsule and stored in a desiccator at 3°C.

During the 2-year study, 276 uredinial isolates were characterized for virulence phenotype: 120 in 1996 and 156 in 1996.

Twelve differentials consisting of 6 to 8 plants of each near-isogenic *Lr* line in a Thatcher background (6) were used in determining the virulence phenotype (*Prt* code) along with near-isogenic lines with *Lr10*, *Lr18*, and *Lr19*. Each virulence phenotype data set for each uredinial isolate was determined on 90 to 120 plants. Urediniospores (4 mg) were suspended in 30 ml Tween 20 and atomized onto 7-day-old primary leaves of the wheat differentials plus the supplemental lines. Two single-pustuled uredinial isolates from each collection in 1995 and three from each collection in 1996 were evaluated for virulence phenotype. Inoculated plants were maintained in a greenhouse at 20 to 25°C with supplemental 400-W metal halide lights.

Infection types were recorded 10 to 12 days postinoculation. The virulence phenotype determinations were repeated for selected uredinial isolates as a check on accuracy of reading the differential sets for infection type. Each uredinial isolate was assigned a three-letter virulence phenotype or *Prt* code based on low (0, 1, or 2) or high (3 or 4) infection type to the 12 differentials and supplemental lines (11). Each three-letter *Prt* code is followed by a hyphen and a listing of ineffective host genes in the supplemental lines.

RESULTS AND DISCUSSION

In 1995 and 1996, leaf rust severities were moderate in wheat fields of eastern and central Nebraska and light in the west central and panhandle regions. Dry conditions in the southern and central plains during April and May were not conducive to leaf rust development, thus less inoculum was available to infect wheat in Nebraska. During both years, leaf rust was not detected in southeastern Nebraska until mid-May; subsequent cool and dry weather slowed its development through the remainder of May and June.

Of the 1995 isolates, 37% were collected in the east, 32% in the central, 19% in the west-central, and 12% in the panhandle regions of Nebraska. The distribution of isolates in the 1996 leaf rust collections was 44% from the east, 33% from the central, and 23% from the west-central. Approximately 70% of the isolates of both years were from field collections in eastern and central Nebraska, where higher rainfall favored leaf rust development.

During 1995 and 1996 in all regions, over 80% of the isolates collected were

Table 2. Virulence frequency[x] by year of the 1992, 1993, 1995, and 1996 *Puccinia recondita* f. sp. *tritici* populations in Nebraska to 12 near-isogenic wheat differentials and three supplemental lines

Lr gene	1992	1993	1995	1996	Change in %/year b[y]
1	100	100	100	100	…
2a	85	77	27	55	–12.52**
2c	85	80	40	55	–10.70**
3	100	100	100	100	…
3ka	0	15	93	85	26.16**
9	0	1	0	9	1.24ns
10	100	100	100	100	…
11	73	74	96	97	6.88**
16	0	0	0	4	0.61ns
17	9	10	0	30	2.30ns
18	100	92	100	94	–0.35ns
19	0	0	—[z]	0	…
24	82	60	58	34	–8.71**
26	53	40	14	1	–12.61**
30	53	63	100	96	12.75**

[x] Represents the percentage of leaf rust isolates collected that year.
[y] b = regression slope over years, … = not analyzed, ** = highly significant, and ns = nonsignificant.
[z] Due to a seed impurity problem, *Lr19* was not included in the 1995 data.

Table 1. Virulence frequency[x] of the 1995 and 1996 *Puccinia recondita* f. sp. *tritici* populations in Nebraska by geographic region to 12 near-isogenic wheat differentials and three supplemental lines

	East		Central		West-central		Panhandle		Mean	
Lr gene	1995	1996	1995	1996	1995	1996	1995	1996[y]	1995	1996
1	100	100	100	100	100	100	100	…	100	100
2a	30	55	25	51	35	61	13	…	27	55
2c	39	55	44	51	39	61	40	…	40	55
3	100	100	100	100	100	100	100	…	100	100
3ka	91	84	89	84	100	86	100	…	93	85
9	0	7	0	17	0	0	0	…	0	9
10	100	100	100	100	100	100	100	…	100	100
11	98	96	100	98	100	100	87	…	96	97
16	0	1	0	6	0	6	0	…	0	4
17	0	29	0	27	0	36	0	…	0	30
18	100	96	100	94	100	89	100	…	100	94
19[z]	…	0	…	0	…	0	…	…	…	0
24	55	52	64	35	61	25	47	…	58	34
26	14	0	22	4	13	0	13	…	14	1
30	100	94	100	96	100	97	100	…	100	96

[x] Represents the percentage of leaf rust isolates collected from that specific region.
[y] Leaf rust was not detected in the panhandle region during 1996.
[z] Due to a seed purity problem, *Lr19* was not included in the 1995 data.

virulent to *Lr1*, *Lr3*, *Lr3ka*, *Lr10*, *Lr11*, *Lr18*, and *Lr30* (Table 1). These results were consistent with that found in the 1992 and 1993 Nebraska surveys (17), where the virulence frequency was high to *Lr1*, *Lr3*, *Lr10*, *Lr11*, and *Lr18* (Table 2). When virulence frequency was regressed over years, they differed from the previous Nebraska surveys in that the virulence frequencies were lower in 1995 and 1996 to *Lr2a*, *Lr2c*, *Lr24*, and *Lr26*, and higher to *Lr3ka*, *Lr11*, and *Lr30* (Table 2). The most dramatic changes occurred in the virulence frequencies to *Lr3ka*, which increased from 0% in 1992 to 93 and 85% in 1995 and 1996, respectively, and to *Lr26*, which showed a decrease from 53% in 1992 to 1% in 1996. Kolmer (5) reports pathogenic variation with *Lr18* where avirulence usually predominates. Our surveys find virulence to *Lr18* in a high proportion of the isolates. Avirulent pathotypes to *Lr18* may appear virulent based on seedling tests at higher (25°C) greenhouse temperatures. Our tests were conducted at greenhouse temperatures of 20 to 25°C, which may account for the high virulence frequency to *Lr18*. McIntosh et al. (11) state that virulence to *Lr21* has not been found in North America; however, Statler et al. (16) found virulence to *Lr21* in a survey in North Dakota in 1982 to 1984. A low infection type (2+) with this gene is hard to decipher, so it is possible that avirulent responses could be interpreted as virulent based on seedling reaction (11); therefore, we chose not to include *Lr21* in our 1995 and 1996 summaries. From 1992 to 1996, virulence frequencies remained relatively unchanged for *Lr1*, *Lr3*, *Lr9*, *Lr16*, and *Lr17* (Table 2). A 1994 survey in Canada (4) also found a high incidence of virulence to *Lr1*, *Lr3*, and *Lr3ka* but only intermediate virulence frequencies to *Lr11* and *Lr18*; *Lr10* was not included in this Canadian survey. Consistent with the Nebraska data (17), virulence frequencies were low to *Lr9* and *Lr16*.

Table 3. Virulence phenotypes of *Puccinia recondita* f. sp. *tritici* isolates collected in Nebraska in 1995[x]

		East		Central		West-central		Panhandle		Total	
***Prt* Code[y]**	**Virulence formula[z]**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
MBH-10,18	1,3,11,30,10,18	1	2.3	1	2.6	0	0	0	0	2	1.7
MBR-10,18	1,3,3ka,11,30,10,18	9	20.5	6	15.8	7	30.4	4	26.7	26	21.6
MCR-10,18	1,3,26,3ka,11,30,10,18	1	2.3	0	0	0	0	0	0	1	0.8
MDM-10,18	1,3,24,3ka,30,10,18	0	0	0	0	0	0	1	6.7	1	0.8
MDR-10,18	1,3,24,3ka,11,30,10,18	11	25.0	7	18.4	4	17.4	4	26.6	26	21.6
MFH-10,18	1,3,24,26,11,30,10,18	0	0	2	5.3	0	0	0	0	2	1.7
MFR-10,18	1,3,24,26,3ka,11,30,10,18	2	4.5	0	0	3	13.0	0	0	5	4.2
MLR-10,18	1,3,9,3ka,11,30,10,18	1	2.3	5	13.2	0	0	0	0	6	5.0
MMR-10,18	1,3,9,26,3ka,11,30,10,18	2	4.5	1	2.6	0	0	0	0	3	2.5
PBR-10,18	1,2c,3,3ka,11,30,10,18	3	6.8	1	2.6	1	4.3	2	13.3	7	5.8
PDR-10,18	1,2c,3,24,3ka,11,30,10,18	1	2.3	5	13.2	0	0	1	6.7	7	5.8
PFR-10,18	1,2c,3,24,26,3ka,11,30,10,18	0	0	1	2.6	0	0	1	6.7	2	1.7
TBH-10,18	1,2a,2c,3,11,30,10,18	1	2.3	0	0	0	0	0	0	1	0.8
TBM-10,18	1,2a,2c,3,3ka,30,10,18	1	2.3	0	0	0	0	1	6.7	2	1.7
TCR-10,18	1,2a,2c,3,26,3ka,11,30,10,18	2	4.5	0	0	1	4.3	1	6.7	4	3.3
TDH-10,18	1,2a,2c,3,24,11,30,10,18	2	4.5	0	0	0	0	0	0	2	1.7
TDR-10,18	1,2a,2c,3,24,3ka,11,30,10,18	7	15.9	3	7.9	5	21.7	0	0	15	12.5
TFH-10,18	1,2a,2c,3,24,26,11,30,10,18	0	0	1	2.6	0	0	0	0	1	0.8
TFR-10,18	1,2a,2c,3,24,26,3ka,11,30,10,18	0	0	3	7.9	2	8.7	0	0	5	4.2
TLR-10,18	1,2a,2c,3,9,3ka,11,30,10,18	0	0	2	5.3	0	0	0	0	2	1.7
Total		44		38		23		15		120	

[x] Number and percentage of isolates from indicated area.
[y] *Prt* code (4) plus *Lr10* and *Lr18* near-isogenic supplemental differentials.
[z] *Lr* genes on which that isolate is virulent.

Table 4. Virulence phenotypes of *Puccinia recondita* f. sp. *tritici* isolates collected in Nebraska 1996[x]

		East		Central		West-central		Total	
***Prt* Code[y]**	**Virulence formula[z]**	**No.**	**%**	**No.**	**%**	**No.**	**%**	**No.**	**%**
MBG-10,18	1,3,11,10,18	1	1.5	1	2.0	1	2.8	3	1.9
MBH-10,18	1,3,11,30,10,18	4	5.8	2	3.9	1	2.8	7	4.5
MBR-10,18	1,3,3ka,11,30,10,18	14	20.3	10	19.6	8	22.3	32	20.5
MBR-10	1,3,3ka,11,30,10	2	2.9	1	2.0	0	0	3	1.9
MBT-10,18	1,3,3ka,11,17,30,10,18	0	0	1	2.0	0	0	1	0.6
MBT-10	1,3,3ka,11,17,30,10	0	0	1	2.0	2	5.6	3	1.9
MDB-10,18	1,3,24,10,18	3	4.3	1	2.0	0	0	4	2.6
MDR-10,18	1,3,24,3ka,11,30,10,18	6	8.7	7	13.8	2	5.6	15	9.7
MDT-10,18	1,3,24,3ka,11,17,30,10,18	1	1.5	1	2.0	0	0	2	1.3
TBH-10,18	1,2a,2c,3,11,30,10,18	2	2.9	4	7.8	1	2.8	7	4.5
TBR-10,18	1,2a,2c,3,3ka,11,30,10,18	8	11.5	7	13.7	6	16.7	21	13.4
TBT-10	1,2a,2c,3,3ka,11,17,30,10	1	1.5	1	2.0	2	5.6	4	2.6
TBT-10,18	1,2a,2c,3,3ka,11,17,30,10,18	11	15.9	4	7.8	7	19.5	22	14.1
TDH-10,18	1,2a,2c,3,24,11,30,10,18	1	1.5	0	0	2	5.6	3	1.9
TDR-10,18	1,2a,2c,3,24,3ka,11,30,10,18	8	11.6	4	7.9	2	5.6	14	9.0
TDT-10,18	1,2a,2c,3,24,3ka,11,17,30,10,18	6	8.7	1	2.0	0	0	7	4.5
TFT-10,18	1,2a,2c,3,24,26,3ka,11,17,30,10,18	0	0	2	3.9	0	0	2	1.3
TJT-10,18	1,2a,2c,3,16,24,3ka,11,17,30,10,18	1	1.5	3	5.9	2	5.6	6	3.8
Total		69		51		36		156	

[x] Number and percentage of isolates from indicated area
[y] *Prt* code (4) plus *Lr 10* and *Lr18* near-isogenic supplemental differentials.
[z] *Lr* genes on which that isolate is virulent.

Since the 1992 Nebraska leaf rust survey, virulence frequency to *Lr24* has declined from 82% in 1992 to 34% in 1996. The decline in virulence frequencies to *Lr24* and *Lr26* could be due to the decline in acreage in the Great Plains of the hard red winter wheat cultivar Siouxland, which has both *Lr24* and *Lr26*. *Lr24* is postulated to be present in the cultivars AgriPro Abiline, Arkan, Cimmaron, Collin, TAM 200, Thunderbird, and Arapahoe, which are still widely grown and may account for the less dramatic decline in virulence to this gene as compared to that for *Lr26* (13). In 1988, Siouxland occupied 21% of the Nebraska wheat acreage, but in 1996 it accounted for only 4% of the total Nebraska wheat acreage. Previous surveys in the United States (7,10) reported an increase in virulence to *Lr24* and *Lr26* during 1988 to 1992.

No virulence was found to *Lr16* and *Lr17* in 1995; however, in 1996 the frequency of virulence was 4% to *Lr16* and 30% to *Lr17*. Data from national (6) and local (10,17) leaf rust surveys also show virulence frequencies from 0 to 30% to these 2 genes, as well as to *Lr9*. The gene *Lr16* provides an intermediate level of protection, as demonstrated by the low infection types ranging from 1 to 3C (11). *Lr16* may interact with other genes to give enhanced levels of resistance. The cultivars Arapahoe and Redland, which contain *Lr16* along with at least one other leaf rust resistance gene (13), comprised 35 and 4%, respectively, of the Nebraska winter wheat acreage in 1995.

Consistent with the 1994 leaf rust survey in Canada (4), we found increased virulence to *Lr3ka* and *Lr30* in 1995 and 1996 compared to our 1992 and 1993 surveys (Table 2). Kolmer reports that the virulences to these 2 genes are tightly linked (4), which may explain their parallel increase. He also attributes the increased virulence to *Lr3ka* to its being used as a leaf rust resistance gene in winter wheats in the United States. *Lr3ka* is postulated to be present in the Kansas cultivars Ike and Karl 92 (USDA Cereal Disease Laboratory, St. Paul, MN, *unpublished*). Both of these hard red winter wheat cultivars are grown in Kansas and in southern Nebraska.

The total number of virulence phenotypes remained essentially unchanged from 1995 to 1996, with the isolates classified into 20 *Prt* codes in 1995 and 18 *Prt* codes in 1996 (Tables 3 and 4). These data compare with 37 and 46 virulence phenotypes characterized in the 1992 and 1993 Nebraska leaf rust surveys (17). Twelve different virulence phenotypes were identified in 1996 that were not found in 1995. The virulence phenotypes are arranged in Tables 3 and 4 by *Prt* code, and results are presented as numbers and percentages of isolates within the various Nebraska wheat production regions. Phenotypes MBR-10,18 and MDR-10,18 were the most common virulence phenotypes in 1995; each accounted for 21.6% of the total leaf rust population. The frequency of MBR-10,18 ranged from 26.7% in the panhandle to 6% in the central region, and MDR-10,18 ranged from 26.6% in the panhandle to 4% in the west-central region. In his 1995 survey, Kolmer (5) reported that the MBR *Prt* code accounted for the highest frequency of virulence phenotypes. The virulence phenotype MBR-10,18 at 20.5% was the most common in 1996. This represents a shift in predominant virulence phenotypes from those characterized in Nebraska in 1992 and 1993. Phenotype TFH-10,18,21 was the most common *Prt* in 1992, and in 1993 phenotype TFH-10,18 was the most common *Prt* code. Virulence phenotype TFH, which contains *Lr24* and *Lr26*, accounted for less than 1% of the total virulence phenotypes characterized in 1995 and was not found in 1996. Conversely, virulence phenotype MBR was not detected in either the 1992 or 1993 Nebraska leaf rust surveys (17). The MBR *Prt* code shows virulence to *Lr3ka*, and the frequency of virulence to that gene increased from 0 and 15% in 1992 and 1993, respectively, to 93 and 85% in 1995 and 1996, respectively. The same trend also occurred for *Lr30*, which is a component of the MBR *Prt* code. The MBR phenotype does not include virulence to *Lr2a* and *Lr2c*, whereas the TFH virulence phenotype does. In 1992 and 1993, virulence frequencies were high to *Lr2a* and *Lr2c* and decreased to an intermediate level in 1995 and 1996.

In summary, we characterized virulence phenotypes in 1996 that were not present in 1995. There have been major shifts in virulence phenotypes and in virulence frequencies to specific *Lr* genes since the 1992 Nebraska leaf rust survey. These shifts in virulence in the natural *P. recondita* population reflect the increased or decreased use of certain *Lr* genes such as *Lr3ka*, *Lr24*, and *Lr 26* in hard red winter wheat cultivars grown in the southern and central plains states. Our survey also has shown that the 1995 and 1996 *P. recondita* populations had a wide range of virulence to the 12 *Lr* differentials and three *Lr* supplemental lines we tested. It shows that gene *Lr3ka* is no longer effective, but that *Lr16* continues to provide resistance. However, to provide a more stable level of leaf rust resistance, this gene might be pyramided with other effective leaf rust resistant genes (3).

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