Resistance to Benzimidazole Fungicides in the Cereal Eyespot Pathogen, *Pseudocercosporella herpotrichoides*, in the Pacific Northwest 1984 to 1990

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ABSTRACT

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Isolates of *Pseudocercosporella herpotrichoides* resistant to benzimidazole fungicides were detected in commercial winter wheat fields in the Pacific Northwest region (Washington, Oregon, and Idaho) of the United States for the first time in the spring of 1989. Benzimidazole-resistant isolates were found in nine of 62 fields sampled in 1989 and in 17 of 167 fields sampled in 1990, which represents 24 and 19% of those fields yielding the pathogen, respectively. In 1989 and 1990, respectively, 96 and 70% of all isolates collected from fields where fungicide resistance was detected were resistant to the benzimidazole fungicides. All fields where fungicide-resistant strains of the eyespot fungus were found had at least four previous applications of a benzimidazole fungicide. In 1989 and 1990, respectively, 24 and 15% of the *P. herpotrichoides* cultures collected had a slow growth rate with feathery colony margins on potato-dextrose agar and corresponded to rye-type isolates. However, benzimidazole-resistant rye-type isolates represented only 7 and 4% of the total resistant isolates collected in 1989 and 1990, respectively.

Additional keywords: *Triticum aestivum*

Eyespot, caused by *Tapesia yallundae* Wallwork & Spooner (anamorph = *Pseudocercosporella herpotrichoides* (Fron) Deighton), is a chronic, yield-limiting disease of winter wheat (*Triticum aestivum* L.) in the Pacific Northwest region of the United States, especially eastern Washington, northeastern Oregon, and northern Idaho (the Inland Pacific Northwest). The pathogen survives in residue from previous infected crops, where it produces conidia that are disseminated by splashing water to nearby plants from autumn through early spring. Eyespot is most prevalent in areas receiving more than 450 mm of annual precipitation; however, in some years eyespot can be severe in areas receiving only 250 mm of annual precipitation. Annually, more than 500,000 ha may be affected by eyespot in this region, of which over 60% may receive a fungicide application for its control.

Prior to 1977, eyespot was controlled primarily by cultural practices such as delaying seeding in the autumn, increasing the time between susceptible crops, and/or growing tolerant cultivars. Since the introduction and registration of Benlate (benomyl; E. I. Dupont De Nemours & Co.) in 1977 for eyespot control in the Pacific Northwest, a single foliar application of a benzimidazole fungicide (Benlate, Mertect [thiabendazole; Merck & Co.], or Topsin-M [thiophanate-methyl; Elf-Atochem North America, Inc.]) in the spring before stem elongation (growth stage 31) (29) has become the standard control practice.

Resistance to the benzimidazole fungicides in several plant pathogenic fungi was reported shortly after their introduction in the 1960s (27). Due to these early reports of fungicide resistance, Chidambaram and Bruehl (7) screened several isolates of *P. herpotrichoides* originating from diverse geographic areas in the Pacific Northwest for resistance to benomyl before its commercial introduction. Although none of the 19 isolates tested was found to be resistant to benomyl, the authors concluded that resistance could still arise in the field. Rashid and Schlösser (23) first detected benzimidazole-resistant isolates of *P. herpotrichoides* in 1974 in Germany. In subsequent work, Rashid and Schlösser (24) found fungicide-resistant isolates of *P. herpotrichoides* in nine of 19 fields that had never received a benzimidazole treatment, and in three of eight fields that had previously received two to four applications of a benzimidazole-containing fungicide. However, they found no cases of fungicide failures due to a lack of disease control, i.e., practical resistance (3), and concluded that a single application of a benzimidazole per year would not lead to problems with fungicide resistance.

Widespread resistance to the benzimidazole fungicides in *P. herpotrichoides* was reported during the 1980s from Denmark (22), France (6,16), Germany (9), Ireland (8), New Zealand (13), the Netherlands (25), and the United Kingdom (4,10,14). Several of these reports noted a reduced ability to control eyespot with benzimidazole fungicides in fields where benzimidazole-resistant isolates of *P. herpotrichoides* were found (6,9,10,16,22). At about the same time that benzimidazole resistance became widespread in *P. herpotrichoides*, colony morphology of the predominant pathogen isolates in Ireland, the Netherlands, and the United Kingdom shifted from those with a relatively fast growth rate and uniform colony margins (fast-even) on potato-dextrose agar (PDA) to isolates with a slow growth rate and uneven or feathery colony margins (slow-feathery) (2,4,8,10,12,14,25). The fast- and slow-growing isolates of *P. herpotrichoides* correspond, respectively, to the wheat-type (W-type) and rye-type (R-type) strains described by Scott et al. (26).

Organized surveys for benzimidazole-resistant strains of *P. herpotrichoides* in the Pacific Northwest were begun in 1983. In 1985, Bruehl et al. (5) reported the first occurrence of benzimidazole-resistant strains of *P. herpotrichoides* from samples collected in experimental field plots in the Pacific Northwest; such occurrences in commercial fields were unknown at that time. The primary objective of these surveys was to determine whether benzimidazole-resistant strains of *P. herpotrichoides* existed in commercial winter wheat fields in the Pacific Northwest region of the United States, and if so, whether their occurrence was associated with specific cultural practices or previous fungicide usage. This report describes the results of surveys conducted during the period from 1983 to 1990. A preliminary report has been published (21).

MATERIALS AND METHODS

Sample collection. Surveys were conducted during the 1984, 1985, 1989, and 1990 crop years. No survey work was conducted during 1986, 1987, and 1988 because of unusually dry weather conditions that resulted in very low disease incidence.

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In 1984 and 1985, commercial winter wheat fields where eyespot was severe and therefore likely to have a benzimidazole fungicide application were identified with the help of county extension agents and agrichemical company field scouts, and sampled directly. For the 1989 and 1990 crop years, self-addressed envelopes containing a questionnaire and sampling directions were distributed to county agents, agrichemical company field scouts, and farmers in areas where fields would be evaluated for possible fungicide application. Information requested on the questionnaire included name and address of the respondent, location of the field, name of the cultivar(s) being grown, cultural practices including rotation crops since the previous winter wheat crop and length of the crop rotation, and previous fungicide use, including whether any failure to control eyespot was apparent.

Samples were collected from February to May during each year of the survey. Approximately six to 10 plants were taken from representative areas within each field when the wheat was in the tillering to pseudostem erection stage of growth (growth stage 23-30) and before a fungicide application was made in that year. Samples were returned to the laboratory, where the plants were washed, stems separated, and the presence or absence of symptoms for each stem recorded.

In 1989 and 1990, follow-up interviews with farmers or field personnel associated with fields having fungicide-resistant isolates were conducted to determine previous fungicide use practices and indications of fungicide failure. In 1989, the number of previous benzimidazole fungicide applications was determined for fields with resistant isolates; whereas in 1990, only the relative intensity of use was determined due to the difficulty in obtaining exact numbers of applications.

Pathogen isolation and identification. Initial isolations were made in the absence of fungicides. Stem segments with symptoms of eyespot were excised, and loose leaf sheaths were removed. The stem pieces were then washed in cold running water for 30 min to 2 h, surface disinfected in a solution of 0.05% NaOCl containing 4 drops of Tween 20 (polyoxyethylene-sorbitan monolaurate) per liter, rinsed in sterile water, placed on water agar (WA; Difco, Detroit, MI, 15 g/liter) containing 50 µg of rifampicin per ml, and incubated at 15°C in the dark or with continuous near-ultraviolet light (to suppress contaminants) (20). After 3 to 10 days, portions of compact, submerged mycelia emanating from the stem pieces were subcultured onto one-fifth strength PDA (0.2× PDA) containing 50 µg of rifampicin per ml and incubated at room temperature (20°C). Colonies having characteristics typical of *P. herpotrichoides* were transferred onto full-strength PDA and incubated at room temperature. One isolate was saved from each stem; thus each isolate represents a different stem from the original sample. A maximum of 25 isolates was collected from a single field. The identity of all new isolates was confirmed by inducing sporulation of cultures grown on WA at 15°C with continuous near-ultraviolet light (15,20) for 1 to 3 weeks. Cultural characteristics and relative growth rate on PDA at room temperature were noted, and isolates were designated as either fast-even or slow-feathery.

New isolates of *P. herpotrichoides* were transferred to PDA slants for short-term storage at 4°C, and onto sterile oat kernels for long-term storage, as soon as possible after isolation (20). For storage on oat kernels, bits of mycelium from PDA cultures were transferred to moist, autoclaved oat kernels (5 ml of dry oats + 2 ml of water) in 10-ml screw cap vials and incubated for 1 to 2 weeks at 20°C until the oats were thoroughly colonized. The oat kernels were then air-dried in uncapped vials under a laminar flow hood, recapped, and stored desiccated at –20°C.

Twenty isolates of *P. herpotrichoides* collected in 1989 and 24 isolates collected in 1990 were tested for pathogenicity to wheat and rye. The isolates were randomly selected from those with fast-even or slow-feathery morphology and those resistant or sensitive to the benzimidazole fungicides. Seedlings were inoculated at the two-leaf stage of growth (growth stage 12) by atomizing a suspension of conidia (1×10^6 conidia per ml) onto the plants until runoff. Disease severity was assessed visually after 4 to 6 weeks of growth at 10 to 13°C with high relative humidity (28).

Testing isolates for fungicide resistance. Blocks of mycelium were cut from the periphery of cultures growing on PDA with a cork borer (8 mm diameter) and transferred, mycelium down, to petri dishes (three blocks per dish) containing 20 ml of PDA + fungicide or control dishes containing PDA + solvent only (the same solvent in which the fungicide was dissolved). All fungicide-amended media were prepared within 48 h of use. Dishes were incubated in covered plastic boxes (to prevent desiccation) on a laboratory bench at 18 to 22°C for 10 to 14 days and then evaluated for growth. Isolates that grew from each of the three inoculum blocks within a dish were considered resistant.

During the 1984, 1985, and 1989 surveys, resistance to benomyl, thiabendazole, and thiophanate-methyl was tested by incorporating formulated Benlate (PNW formulation in 1984 and 1985, and 80DF formulation in 1989), Mertect (340-F formulation in 1984 and 1985, and DF formulation in 1989), or Topsin-M (70WP formulation in 1984, 1985, and 1989) suspended in water and added to a final concentration of 3 µg a.i./ml. Since cross-resistance exists among these benzimidazole fungicides, isolates were tested, in 1990 only, for resistance to carbendazim, which was added as technical grade material (98% purity) dissolved in methanol and added to a final concentration of 1 µg a.i./ml.

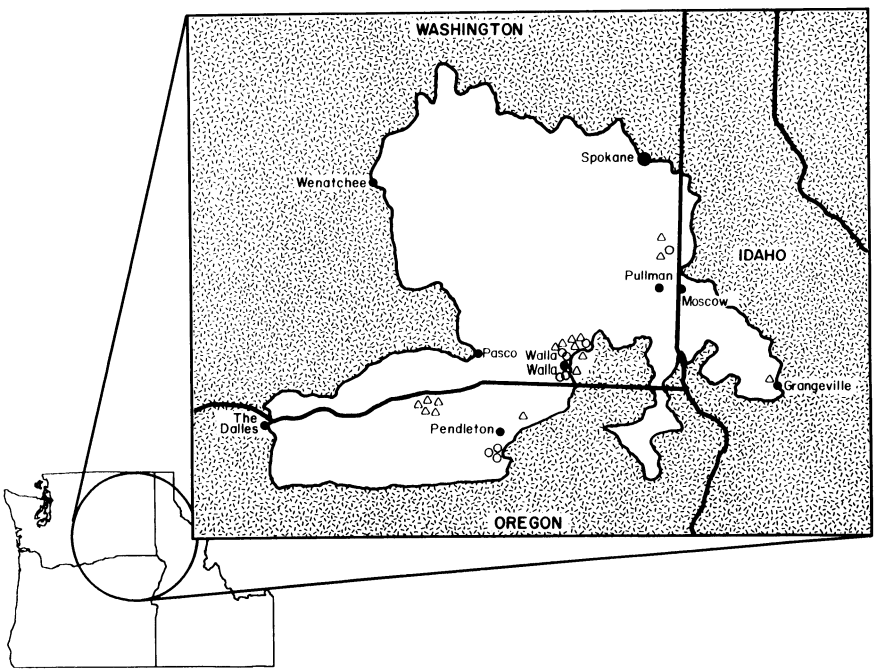

Fig. 1. Distribution of winter wheat fields in the Pacific Northwest where benzimidazole-resistant strains of *Pseudocercosporella herpotrichoides* were found. The unshaded area represents the inland Pacific Northwest wheat production area. Circles (O) and triangles (Δ) denote fields from which fungicide-resistant strains were isolated in 1989 and 1990, respectively.

RESULTS

1984 and 1985. *P. herpotrichoides* was isolated from 12 of 16 fields sampled in

1984 and 16 of 20 fields sampled in 1985, yielding a total of 124 isolates. None of the isolates collected during these 2 years was resistant to the benzimidazole fungicides tested.

1989. Cold temperatures during the winter of 1988–89 resulted in winter-killing of approximately 70% of the winter wheat crop in the Pacific Northwest. Samples were received from 62 fields, 37 of which yielded a total of 279 isolates of *P. herpotrichoides*. Benzimidazole-resistant isolates were found in nine fields, or 24% of those yielding the pathogen. Six of the fields with benzimidazole-resistant isolates were located in Washington and three were in Oregon (Fig. 1, Table 1). The percentage of benzimidazole-resistant isolates in these nine fields ranged from 67 to 100% (Table 1). All of the benzimidazole-resistant isolates exhibited cross-resistance to benomyl, thiabendazole, and thiophanate-methyl.

Sixty-seven isolates (24% of the total) from 15 fields had a slow growth rate with feathery colony margins on PDA; eight of these (12%) were resistant to the benzimidazole fungicides. Pathogenicity tests conducted on wheat and rye confirmed that slow-feathery isolates were equivalent to R-type isolates (18) described by Scott et al. (26).

The cultural practices used in the nine fields with fungicide-resistant isolates of *P. herpotrichoides* were representative of those used throughout the region and ranged from crop rotations in which winter wheat was grown once every 2 or 3 years with natural precipitation only (fields 18 and 62), to very intensive management where winter wheat was grown continuously for up to 11 years (fields 44 to 46) before crop rotation, with irrigation (Table 2). All of the fields with fungicide-resistant isolates had at least five previous applications of a benzimidazole fungicide for eyespot control. There was no apparent correlation between the specific fungicide used and occurrence of resistance. Prior to 1989, there were no indications of a fungicide failure in these fields based on observations of lodging and lack of yield response following fungicide application by the farmer. In 1989, however, seven fields (44 to 46 and 52 to 55) experienced varying degrees of failure, based on the occurrence of widespread lodging and yields far below the long-term averages for the respective fields. Practical resistance was confirmed in field 44 the following season when a fungicide efficacy trial was conducted in this field (19).

1990. Samples were received from 167 fields, of which 90 yielded a total of 398 isolates of *P. herpotrichoides*. Benzimidazole-resistant isolates were found in 17 fields, or 19% of those from which the pathogen was isolated. Nine fields with resistant isolates were located in Washington, seven in Oregon, and one in Idaho (Fig. 1, Table 3). The percentage of benzimidazole-resistant *P. herpotrichoides* isolates in these fields ranged from 18 to 100%. Fifty-nine isolates (15% of the total) from 16 fields had a slow growth rate with feathery colony margins on PDA, but only two of these isolates (3%) were resistant to the benzimidazole fungicides.

As in 1989, a wide range of cultural practices representative of those used throughout the region had been used in the fields yielding benzimidazole-resistant isolates of *P. herpotrichoides* (Table 4). All of the fields where resistant isolates were found had previously received from four to

Table 1. Winter wheat fields in which benzimidazole-resistant isolates of *Pseudocercosporella herpotrichoides* were detected in the Pacific Northwest in 1989

Field	Location	Isolates (no.)	Resistant isolates (no.)		% Resistant
			Fast-even[a]	Slow-feathery	
18	Dayton, WA	7	6	0	86
44	Pendleton, OR	40	32	7	98
45	Pendleton, OR	2	2	0	100
46	Pendleton, OR	3	2	0	67
52	Walla Walla, WA	8	7	1	100
53	Walla Walla, WA	6	6	0	100
54	Walla Walla, WA	26	24	0	92
55	Walla Walla, WA	8	8	0	100
62	Garfield, WA	18	18	0	100
	Total	118	105	8	

[a] Fast-even and slow-feathery isolates correspond to wheat-type and rye-type isolates, respectively (26).

Table 2. Crop rotation, irrigation, and previous fungicide use in nine winter wheat fields where benzimidazole-resistant isolates of *Pseudocercosporella herpotrichoides* were detected in the Pacific Northwest in 1989

Field	Rotation[a]	Irrigation[b]	Previous fungic. applic. (no.)	Previous failures[c]
18	WW - SC - F	No	5	No
44	WW - WW - WW[d]	Yes	7	Yes
45	WW - WW - WW[d]	Yes	7	Yes
46	WW - WW - WW[d]	Yes	7	Yes
52	P - WW - WW	Yes	7-8	No
53	WW - WW- WW	Yes	7-8	No
54	P - WW - WW	Yes	7-8	No
55	WW - P - WW	Yes	7-8	No
62	WW - L - WW	No	5-6	No

[a] Previous crops: WW = winter wheat; SC = spring wheat or barley; P = peas; L = lentils; F = fallow.
[b] No = rain-fed precipitation only; Yes = supplemental irrigation was used to some extent, ranging from one preplant and one spring irrigation to multiple applications during the season.
[c] Previous indications of a fungicide failure were determined by interviewing farmers and field scouts about yield and lodging in previous crops treated with a fungicide for eyespot control.
[d] These fields had been cropped to winter wheat for 10 consecutive years at the time of sampling.

Table 3. Winter wheat fields in which benzimidazole-resistant isolates of *Pseudocercosporella herpotrichoides* were detected in the Pacific Northwest in 1990

Field	Location	Isolates (no.)	Resistant isolates (no.)		% Resistant
			Fast-even[a]	Slow-feathery	
7	Walla Walla, WA	8	8	0	100
18	Waitsburg, WA	5	4	0	80
20	Waitsburg, WA	4	4	0	100
23	Umatilla, OR	5	5	0	100
25	Walla Walla, WA	11	2	0	18
27	Umatilla, OR	8	8	0	100
28	Umatilla, OR	2	2	0	100
45	Umatilla, OR	10	2	0	20
47	Waitsburg, WA	7	3	0	43
49	Umatilla, OR	1	1	0	100
57	Waitsburg, WA	1	1	0	100
59	Waitsburg, WA	3	1	0	33
80	Grangeville, ID	3	2	1	100
104	Oakesdale, WA	3	2	1	100
124	Garfield, WA	3	3	0	100
162	North Plains, OR	3	3	0	100
168	Adams, OR	2	2	0	100
	Total	79	53	2	

[a] Fast-even and slow-feathery isolates correspond to wheat-type and rye-type isolates, respectively (26).

12 applications of a benzimidazole fungicide for eyespot control. Three of these fields had prior indications of fungicide failures based on lodging and lack of yield response following the fungicide application. None of these fields apparently experienced complete fungicide failures during the 1990 season.

DISCUSSION

The discovery of benzimidazole-resistant isolates of *P. herpotrichoides* in 24% of the fields sampled in 1989 is the first evidence for fungicide resistance in commercial winter wheat fields in the Pacific Northwest. A previous report by Bruehl et al. (5) demonstrated the potential for development of benzimidazole resistance in *P. herpotrichoides* under what was believed to be relatively low selection pressure of the wheat production systems common in the Pacific Northwest, i.e., a single benzimidazole application once every 2 or 3 years. However, the fact that 19% of the winter wheat fields sampled in 1990 yielded benzimidazole-resistant strains of *P. herpotrichoides* suggests that resistance to the benzimidazole fungicides is well-established in this region. It is apparent that even with moderate use of the benzimidazole fungicides, i.e., five applications in 12 years, the selection pressure for fungicide resistance is strong enough to enable detection of resistant isolates with relative ease. In contrast to other reports (1,4,14,24), benzimidazole-resistant strains of *P. herpotrichoides* were found only in fields with a previous history of benzimidazole fungicide application for eyespot control. In several fields where wheat management was more intensive (i.e., short crop rotations with irrigation), fungicide-resistant isolates were present in a high enough proportion to significantly reduce the efficacy of the benzimidazole fungicides, resulting in yield losses (19).

A precise estimate of the proportion of fungicide-resistant isolates within fields was not obtained because we relied on samples submitted by field scouts and therefore could not be certain that the samples were representative of the entire field from which they were taken. However, in 22 of the 26 fields where fungicide resistance was found in 1989 and 1990, over 60% of the isolates collected were resistant to the benzimidazole fungicides. In other studies (9–11,14), an increasing number of previous fungicide applications was positively correlated with the proportion of resistant isolates within a field. Although we could not make this same correlation, we only found benzimidazole-resistant pathogen isolates in fields that had received four or five previous fungicide applications. This finding does not preclude the existence of fungicide-resistant strains of *P. herpotrichoides* in Pacific Northwest wheat fields that have never received a fungicide application.

Practical resistance, which was found in seven fields in 1989, occurred in fields intensively managed for winter wheat production. All of the fields where practical resistance was detected had been cropped consecutively to winter wheat from 3 to 11 years and had received up to eight applications of a fungicide for eyespot control. King and Griffin (14) indicated that 30% fungicide-resistant isolates in a population represented a threshold for fungicide failure. All of the seven fields where disease control failures occurred in 1989 had greater than 60% resistant isolates, and six had more than 90%. Based on the percentages of resistant isolates detected in 1990, it is likely that practical resistance is more widespread than was detected, and that many more disease control failures will occur, especially if benzimidazole fungicides continue to be applied for eyespot control.

Different methods exist for the detection of fungicide-resistant strains of *P. herpotrichoides* (9). Previous studies (1,14) have demonstrated that both mass mycelial isolates and conidia collected from infected stem bases provide reliable estimates of benzimidazole resistance in *P. herpotrichoides*. Tests of conidia are quicker, but mass mycelial isolations in the absence of fungicide were selected for this study to provide reference strains that could be later characterized, and to reduce the possibility of selecting fungicide-resistant strains that arose following exposure to the fungicide in vitro. Preliminary tests with mycelial isolates demonstrated the potential for occasionally selecting such resistant strains when a single inoculum block per isolate was tested. Therefore, three inoculum blocks per isolate were tested, and an isolate was considered resistant only when growth occurred simultaneously from all three blocks. Isolates growing from only one or two of the blocks were restarted from the colonized oat kernels used for long-term isolate storage and retested. Most of these isolates were subsequently found to be benzimidazole sensitive.

Prior to this survey, R-type isolates of *P. herpotrichoides* had not been reported from the Pacific Northwest (18). R-type isolates were found infrequently and represented only 24 and 17% of the isolates collected in 1989 and 1990, respectively. The benzimidazole-resistant R-type isolates represented only 7 and 3% of the total fungicide-resistant isolates collected in 1989 and 1990, respectively (Tables 1 and 3). A chi-square analysis of the proportion of benzimidazole-sensitive and -resistant W- and R-type isolates revealed that statistically ($P = 0.05$) there were disproportionately fewer benzimidazole-resistant R-type than W-type isolates found in both 1989 and 1990. Thus, it appears that there has not been strong selection pressure for R-type isolates in the Pacific Northwest as has occurred elsewhere (12).

R-type isolates of *P. herpotrichoides* and resistance to benzimidazole fungicides were rare in Europe before 1981, being found only in areas with long histories of rye production (12,26). After 1981, however, both R-type isolates and benzimidazole resistance became much more common and widespread (12). In some areas, including England, Wales, Ireland, the Netherlands, and Denmark, benzimidazole resistance was largely associated with R-

Table 4. Crop rotation and previous fungicide use in 17 winter wheat fields where benzimidazole-resistant isolates of *Pseudocercosporella herpotrichoides* were detected in the Pacific Northwest in 1990

Field	Rotation[a]	Previous fungicide use (12 yr)	Previous failures[b]
7	WW - F - WW	<4	No
18	F - WW - WW	5-7	No
20	WW - F - WW	5-7	No
23	WW - WW - WW[c]	12	No
25	WW - P - WW	<4	No
27	WW - P - WW	10	No
28	WW - P - WW	5-7	Yes
45	WW - F - WW	5-7	No
47	WW - F - WW	5-7	No
49	WW - F - WW	5-7	No
57	WW - WW - WW[c]	>8	Yes
59	WW - F - WW	5-7	No
80	SC - F - WW	4	No
104	WW - L - WW	5-7	No
124	SC - P - WW	<4	No
162	WW - C - WW	5-7	No
168	WW - P - WW	5-7	Yes

[a] Previous crops: WW = winter wheat; SC = spring wheat or barley; P = peas; L = lentils; C = corn; F = fallow.

[b] Previous indications of a fungicide failure were determined by interviewing farmers and field scouts about yield and lodging in previous winter wheat crops.

[c] Fields 23 and 57 had been cropped to winter wheat for 10 and 6 consecutive years, respectively, at the time of sampling.

type isolates (2,4,8,10,12,14,25); whereas in other areas such as New Zealand, France, and Germany, benzimidazole resistance was more prevalent in W- than R-type isolates (2,13). Several hypotheses have been advanced to explain the shift in cultural–pathogenic types concomitantly with the shift from benzimidazole sensitivity to resistance. The two factors most often associated with the increased prevalence of R-type isolates are the frequency of winter barley in the crop rotation and the relative sensitivity of W- and R-type isolates to sterol biosynthesis inhibiting fungicides used for foliar disease control (2,10,12,14,17). The positive correlation between the number of previous winter barley crops and frequency of isolation of R-type isolates (10,12,14) was thought to be a result of increased pathogenicity of R-type isolates to barley compared with W-type isolates (26). The increased production of winter barley in Great Britain during the late 1970s and early 1980s thus provided an opportunity for an increase in R-type relative to W-type isolates. Triadimenol fungicide use for foliar disease control increased through the 1970s into the 1980s (2). R-type isolates are less sensitive to triadimenol than W-type isolates (17), and although not used for eyespot control, the presence of this material may have allowed R-type isolates to proliferate.

Winter barley production in the Pacific Northwest is limited to a small fraction of the total cereal producing area. Application of triazole fungicides in general, and triadimenol in particular, for foliar disease control is infrequent and also limited to a small proportion of the total area. Thus, whether benzimidazole-resistant R-type isolates will increase in prevalence in the Pacific Northwest *P. herpotrichoides* population remains to be seen; at this point they are relatively uncommon.

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