White Blotch Incited in Wheat by Bacillus megaterium pv. cerealis

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ABSTRACT

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White blotch of wheat is characterized by severe white to very light tan blotches and streaks on leaf blades, sheaths, and culms. It has occurred with increased frequency on hard red spring, hard red winter, and durum wheats throughout North Dakota since 1975. Bacillus megaterium pv. cerealis was consistently isolated from these blotches and from 2 to 14% of seed of severely affected cultivars. Koch's postulates were completed with 12 strains of the bacterium. On susceptible cultivars, disease symptoms began as small

white or yellow diffuse blotches without water congestion and developed into severe spots within 2-20 days after inoculation. Symptom expression was accelerated by high temperatures and high light intensities. *Pseudomonas syringae* pv. *syringae* caused similar white blotches and streaks, but differed in that the lesions first appeared as transient water-soaked streaks and in the reported degree of virulence on some cultivars.

Additional key words: glumes, barley, oats.

Since 1975, white to very light tan, irregularly shaped lesions, herein labeled 'white blotch,' have appeared at many locations on an increasing number of hard red spring (HRS), hard red winter (HRW), and durum (D) wheat cultivars in North Dakota. Symptoms began, following the boot stage of plant development, as small yellow or white lesions that quickly enlarged into white or very light tan, irregular blotches and streaks on leaf blades, sheaths, and culms. Severity of damage on susceptible cultivars was comparable to levels of fungus leaf spot damage that result in economic yield losses in North Dakota (18). Preliminary observations suggested that the white blotches were often broader than the streaks (bacterial leaf necrosis) caused by *Pseudomonas syringae* pv. *syringae* Van Hall and lacked the water-soaking initially associated with the latter (34).

The objective of this study was to determine the etiology of the broader white blotches on wheat (19,20).

MATERIALS AND METHODS

Isolation of the bacillus. In 1977, pathogenic strains WB 19, WB 27, and WB 28 of Bacillus megaterium de Bary were isolated from yellow to white blotches by rinsing leaves for 30 min in running tap water and transferring 1-mm² pieces of lesioned tissue to potato-dextrose agar (PDA). Recovery of this large-celled, chain-forming type of B. megaterium was enhanced when leaves were rubbed gently for 1 min in warm tap water containing 0.1% liquid Ivory (Procter & Gamble, Cincinnati, OH 45202) or San-O-Dis detergent (National Purity Soap and Chemical Co., Minneapolis, MN 55414) and rinsed for 1 min in running warm tap water before being plated on PDA. Strains of the bacterium isolated from field and glasshouse plants were labeled with WB numbers; strains reisolated while confirming pathogenicity via Koch's postulates were labeled with WBr numbers.

Identification of the bacillus. Cells of strains WB and WBr were

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examined for unstained globules, following exposure to aqueous fuchsin (27), for Gram reaction and for spore and vegetative cell morphology with bright-field microscopy. WB 28 and WBr 57 (its strain reisolated while completing Koch's postulates) were mounted on cover glasses, which were attached to the mounting stub with aluminum paint, and prepared for scanning electron microscopy by three different procedures: air dried; adhered with poly-lysine and air dried; or adhered with poly-lysine, fixed in 2.5% glutaraldehyde, dehydrated in an ethyl alcohol series, and criticalpoint dried. Bacteria were viewed with a JEOL model JSM 35 scanning electron microscope and recorded on Polaroid 55 P/N film. Lengths and widths of bacterial cells were measured from the electron micrographs with a Ladd Digitizer and a Monroe calculator. Similar measurements were made of stained and unstained cells with a phase-contrast microscope. Twenty WB and WBr strains, five American Type Culture Collection (ATCC) Bacillus species as procedural checks, and Agrobacterium tumefaciens (E. F. Sm. & Townsend) Conn. from J. L. Swezey as a Gram reaction check, were subjected to species identification tests (Table 1) (6,7,15,16,27).

Pathogenicity trials. Standard inoculum suspensions were prepared by mixing bacteria (from 24-hr-old PDA or nutrient agar cultures grown at 24 or 27 C) in sterile deionized water and adjusting concentrations by dilution plate count and light transmittance at 670 nm. Each WB and WBr strain was adjusted to 8×10^5 colony-forming units (averaging 4.6 cells in chains) per milliliter of water, equivalent to 3.7×10^6 cells per milliliter. B. megaterium ATCC 14581 was adjusted to 3.7×10^6 cells per milliliter. P. syringae pv. syringae virulent strain Ps 488 from J. D. Otta (12) and similar Ps 35 from a white spot on wheat in North Dakota were adjusted to 2.8×10^7 cells per milliliter.

In the first set of 14 inoculations, wheat cultivars were grown in autoclaved soil in clay pots (one plant per pot). Plants at the boot to early dough stages of development were placed in sunlit glasshouse mist chambers for 24–48 hr at 23 ± 5 C before and/or for 24–72 hr after inoculation. Four to 10 plants of each cultivar were inoculated either by dipping their leaves in or spraying their leaves with a standard bacterial suspension. Check plants were treated similarily with sterile deionized water or left untreated. The plants from each treatment were placed in the same sunlit glasshouse mist chamber for the first two trials and in separate mist chambers in separate

glasshouses for the remaining 12 trials. After the plants were misted, they were placed on benches in glasshouses. Severity of spotting was expressed and rated 2-20 days after inoculation and compared to field reactions (Table 2) (34). Since moderate to severe spotting occurred on check plants in 7/14 of the trials, 13 batches of seed from cultivars that were either severely affected or symptomless were selected under the dissecting microscope for soundness and freedom from blemishes. These seeds were either left untreated, soaked in sterile deionized water at 19 C for 6 hr and then at 55 C for 10 min, or surface sterilized in 1% sodium hypochlorite containing three drops of 95% ethyl alcohol per 100 ml for 1 min and rinsed in sterile deionized water. Treated and untreated seed were placed on PDA at 24 and 27 C and on King's medium B (24) at 24 C in petri plates. For 14 days the seeds and any seedlings they produced were checked for growth of B. megaterium and P. syringae (Table 3). The resulting seedlings of L1 HRS wheat (Lee × Minn II-59-8) (very susceptible to white blotch) that appeared to be free of microorganisms on PDA were grown in autoclaved pots of soil in the glasshouses. In 15 trials, two to four plants in the two-leaf seedling stage to the kernel milk stage of plant development were streaked with 24-hr-old bacterial cultures by using a cotton swab or culm injected with 1 ml of standard inoculum. Plants were placed directly on glasshouse benches without wetting the foliage. Each treatment was done on different benches in the same glasshouse or in widely separated glasshouses not used for growing wheat. The check plants were streaked or injected with sterile deionized water or with B. megaterium ATCC 14581, streaked with PDA, or left untreated. Mites and insects were controlled to minimize possible transfer of pathogens. Plants were observed for spotting for at least 20 days after inoculation or until

TABLE 1. Characterization of 20 WB and WBr Bacillus strains

Test	Twenty strains*	Reference strains ^b						
		1	2	3	4	5		
Unstained globules								
in protoplasm	+	+	-	+	+	-		
Crystalline para-								
sporal bodies	-	7.7	-	-	-	-		
Catalase reaction	+	+	+	+	+	+		
Anaerobic growth	_	-	_	+	+	Weak to negative		
Voges Proskauer						negative		
(V-P) reaction	-		+	+	+	+		
pH in V-P broth	5.5-6.5	5.5	6.0-6.5°	7°	6°	5.5		
Growth at 50 C	-		2-	-	5-5	+		
Growth at 65 C	_		-	_		_		
Egg-yolk reaction	-	-	-	+	+	-		
Growth in 0.001%								
lysozyme ^c	-	\rightarrow	+	+	+	+		
Growth in 5%								
NaCl	+	+		+	Weak	+		
Growth in 7%	-	Weak to	_	+	Weak to	+		
NaCl		negative			negative			
Growth in 10%								
NaCl	-	-		-	$(-1)^{2}$	+		
Acid from glucose	+	+	+	+	+	+		
Gas from glucosed	-	-	ND	ND	ND	ND		
Acid from								
mannitol	+	+	+	+	+	+		
Starch hydrolysis	+	+	1-2	+	+	+		
Growth in Koser's								
Citrate	+	+	121	+	+	+		

^a WB 19, 27, 28, 31, 138, 145, 148, 171, 215, 228, and WBr 3, 36, 55, 57, 65, 69, 80 from wheat leaves; WB 227 from a wheat glume; WB 106 from oat leaves; and WB 157 from barley leaves.

seed ripened.

Further pathogenicity tests were made by inoculating leaves of one to four white burley tobacco plants, *Nicotiana tabacum* L., in the 8- to 11-leaf stage of plant development. The leaves of plants were streaked with 24-hr-old bacterial cultures from PDA by using a cotton swab or were injected with 0.2-1.0 ml of standardized suspensions of bacteria grown on PDA for 24 hr at 27 and 35 C.

Additional studies. White blotches in wheat leaves were cryofractured, critical-point dried, and examined for bacteria by scanning electron microscopy.

RESULTS

Field observations. Except for a 1971 occurrence on many durums at Langdon, ND, severe leaf spotting resembling white blotch appeared on only a few cultivars (particularly HRW wheats) at a few locations in North Dakota from 1969 to 1975. Since 1975, symptoms have been observed at many locations on an increasing number of HRS, HRW, and durum wheat cultivars (Table 2). Some cultivars that were resistant from 1975 to 1977 developed symptoms in subsequent years (Table 2). B. megaterium pv. cerealis was consistently isolated from the white blotches, and bacteria resembling P. syringae pv. syringae were less commonly isolated. Disease severity on some, but not all, cultivars was similar to that attributed to P. syringae pv. syringae in South Dakota and Montana (34,37, and Table 2).

Isolation of the bacillus. To date 337 WB strains and 87 WBr strains have been isolated from the initial yellow to white spots as well as from the subsequent, more enduring white to very light tan spots and streaks on wheat leaves and culms in fields and glasshouses (Fig. 1). Three WB strains were isolated from other sources. WB 106 was isolated from greenish-gray lesions on Dal oat (Avena sativa L.) leaves. WB 157 was isolated from white spots on barley (Hordeum vulgare L.) leaves. WB 227 was isolated from dark streaks on wheat glumes. Gently rubbing spotted leaves in warm water containing detergent and then rinsing in warm tap water greatly increased the frequency of isolation of WB (includes WBr) strains from white blotched leaf pieces. Prior to the use of this procedure microorganisms were isolated from white blotches in only low percentages. WB strains were not obtained from tap water and/or detergent solutions. A very few were obtained from nonspotted leaves.

Also isolated from white spots and streaks on wheat leaves were 65 bacterial strains that resembled *P. syringae* in that they were composed of small, Gram-negative rods, formed white colonies that fluoresced on King's medium B, and, when a representative was tested in Koch's postulates (strain Ps35 from the field), caused white spotting and streaking.

Identification of the bacillus. All 427 WB and WBr strains had white, smooth colonies of large, chain-forming vegetative cells that by light microscopy resembled in appearance and measurements WB 28 and its reisolated strain, WBr 57 (Fig. 2). In electron micrographs (Fig. 3) 200 cells of these latter two strains had cell lengths averaging 3.5 μ m (range 1.5 to 7.0 μ m) and cell widths averaging 1.8 μ m (range 1.1 to 2.9 μ m). No appreciable differences in lengths and widths were detected among cells subjected to the three different procedures of preparation for electron microscopy. All 427 strains were Gram-positive, had ellipsoidal spores that did not swell the vegetative cell, and contained smaller globules in the protoplast (Fig. 2). Sometimes only the spores could be found in subculture. The strains were nonmotile and their vegetative cells were in chains; large circular protrusions appeared on the cells prepared for scanning electron microscopy (Fig. 3). In procedural checks, a strain of A. tumefaciens was Gram-negative and Bacillus check strains (Table 1) were Gram-positive. Twenty WB and WBr strains, including the strains from wheat glumes, oats, and barley, were identified to species and resembled B. megaterium more than any other Bacillus (Table 1) (15,16,21).

Pathogenicity trials. In the first 14 pathogenicity trials with plants that had not been tested for presence or absence of bacteria by germination on PDA, inoculations with WB and WBr strains resulted in none to slight spotting on some cultivars and consistent

^bAmerican Type Culture Collection: 1, Bacillus megaterium 14581; 2, B. brevis 8264; 3, B. cereus 14579; 4, B. cereus subsp. mycoides 6462; and 5, B. subtilis 6051.

United States Biochemical Corp., Cleveland, OH 44128.

^dOnly WB 28, WBr 3, and *B. megaterium* ATCC 14581 were tested for production of gas from glucose in Enterotubes II. (Hoffman-La Roche Inc., Nutley, NJ). ND = Not determined.

Reaction differed from that in the literature (15).

TABLE 2. Relative severity of white blotching and streaking on wheat cultivars in the field and glasshouse in North Dakota

Cultivars	Natural field infection 1975–1981 ^a	Bacillus megaterium pv. cerealis strains in glasshouse									
		WB 19	WB 27	WB 28	WB 29	WB 30	WB 31	WB 148	WBr	WBr 57	WBR ^b 100
Winter wheats											
Winoka	5° 5	3	4	_	3	1	4	_	_	4	4
Froid	5	_	4	4	4	4	4	_	_	4	4
Winalta	5	3	4	1	1	3	i	_	200	i	4
Minter	5	4	_	_	2	_	4	_	_	-	-
Trapper	4	_	-	-	-		-	_	-	_	_
Centurk	4,1	1	1	1	1	1	Í	_	_	1	4
Rough Rider	4,1	1	i	i	i	î	î	_	_	2	4
Bronze	4,1	_	<u></u>	-	_	-	-	_	-	4	4
Ekland	4,1	-	-	-	-	_	0-0	_	_	7	7
Lancer	3	-	_	_	2.2	79.00	_	_	-		1
Gent	3									2	4
Agate	2	-	-	-	_	_	-	_	122	3	4
Sundance	1	_	_	_	_	-		-	-	1	1
Spring wheats											
LI	5	4 ^b	4	4		-	5 ^b	4	4	5	
Bonanza	5,1	i	ī	7	1	1	5	-	4	3	5
Waldron	4,1	_	-	Ŷ	_	-			122		-
Era	3	_	-		_	200	1	200	-	1	1
Cateau	3	_	_	1	_	_		30	277	2	_
Olaf	3,2	_	_	î	_	_			-	_	2
Ellar	3,1	_	_		225			220		_	_
Bounty 208	1	1	_	1	1	1	1	-	177	-	-
Chris	i	_	_	-	_	-	_		1999		
Marquis	i	_	1	1			_	1	1	1	-
Lew	i	-	-	-	-	_	-	-	-	1: ::	1
Durums											
Ward	4	4	_	1		_	1	_	-	2	
Rugby	4,2	4	_	î	_		4		_	2	1

^a B. megaterium pv. cerealis was the pathogen most commonly isolated from these blotches; P. syringae pv. syringae-like bacteria were less commonly isolated. Double ratings (example 4,1) indicate little or no symptoms under severe disease conditions for several location-years, but symptoms sometimes since 1978.

yellow to white spots that developed into severe white blotches and streaks on other cultivars. Occasionally, persistent gray-green or yellow blotches developed on some selections. In four of these trials no blotches developed on water-inoculated or uninoculated check plants; in three, slight spotting occurred; and in seven, moderate to severe white blotching and streaking occurred. The bacillus was reisolated from the white blotches and streaks, but only rarely from unspotted leaves. Observations from these trials were compared to 1975-1981 field observations (Table 2).

When seed was tested as a source of WB strains, which might be causing the blotching in the above check plants, strains grew onto PDA from low percentages of untreated, hot water-treated, and surface-sterilized seed of cultivars susceptible to white blotch, but strains rarely grew from seed of more resistant cultivars (Table 3). Bacteria resembling P. syringae bacteria were not found associated with these seeds. The seeds turned black and did not germinate on King's medium B. Moderate to high percentages of the seeds germinated on PDA.

When susceptible L1 plants, from which microorganisms did not grow onto PDA, were grown and used for a second set of 15 pathogenicity trials, approximately 50% of the leaves of post-bootstage plants developed severe white blotches and streaks 2-20 days after swab or syringe inoculation. Leaves of seedlings rarely developed severe white blotches; blotches usually developed only after the plants had grown beyond the jointing stage. Bacillus strains from wheat, oats, and barley grown at 27 and 35 C (WB 19, WB 27, WB 28, WB 106, WB 138, WB 148, WB 157, WBr 3, and WBr 57) and strains of Pseudomonas from wheat (Ps 488 and Ps 35, which grew at 27 but not 35 C), tested in both streak and

TABLE 3. Field occurrence of white blotch and the frequency of the pathogen in treated and untreated seed

Cultivar or selection	White blotch	Seed treatment	Seed with Bacillus megaterium pv. cerealis		
LI HRSª	Commonly very severe	Hot water 1% NaClO None	10/162 11/288 12/84	(6.2%) (3.8%) (14.3%)	
Froid HRW	Commonly very severe	Hot water 1% NaClO	7/72 1/48	(9.7%) (2.1%)	
Winoka HRW	Commonly very severe	Hot water 1% NACIO	5/72 0/48	(6.9%) (0.0%)	
Duri HRS	Occasionally severe	1% NaClO None	1/12 0/12	(8.3%) (0.0%)	
Botno D	Occasionally severe	1% NACIO	0/24	(0.0%)	
BH1146 HRS	Occasionally severe	1% NaClO None	0/12 0/12	(0.0%) (0.0%)	
Waldron HRS	Occasionally severe	1% NaClO	0/12	(0.0%)	
ND 487 HRS	Trace	Hot water 1% NaClO	1/10 0/14	(10.0%) (0.0%)	
Cando D	Trace	1% NaClO	1/10	(10.0%)	
F8012110 HRS	Trace	1% NaClO	0/24	(0.0%)	
Wells D	None	1% NaClO None	0/36 0/12	(0.0%) (0.0%)	
D77197 D	None	1% NaClO	0/36	(0.0%)	

^aHRS = hard red spring wheat, HRW = hard red winter wheat, and D = durum.

^bSpecific strain causing symptoms in doubt because of moderate to severe symptoms on check plants.

Infection rating scale: 5 = 50 - 100% of flag leaves necrotic; 4 = 25 - 50% of flag leaves necrotic; 3 = 10 - 25% of flag leaves necrotic; 2 = 10% or less necrosis on an occasional flag leaf; and 1 = either a trace of or no necrotic lesions on flag leaf.

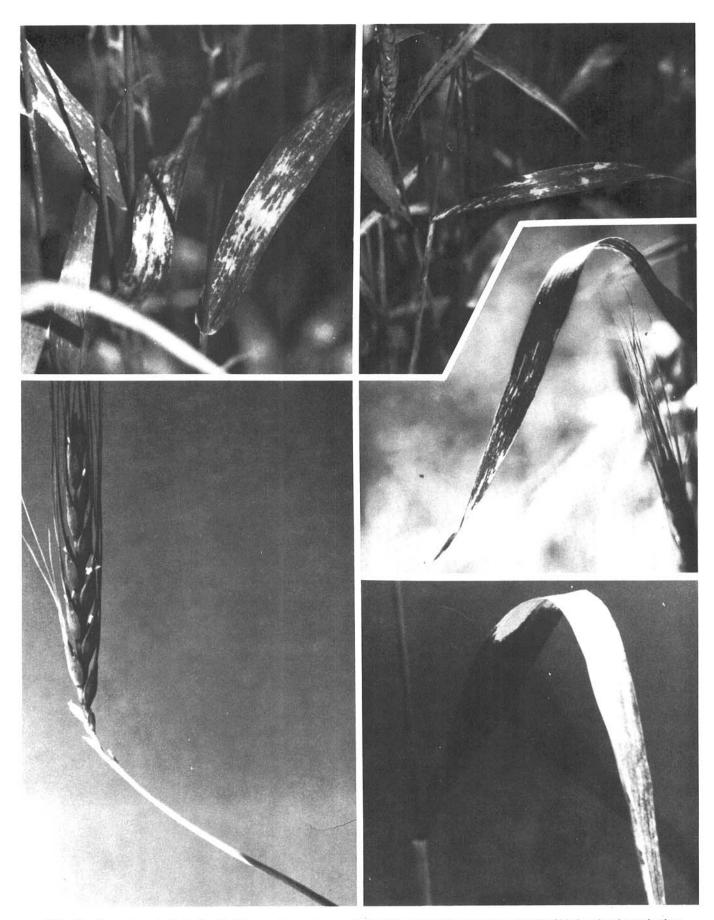


Fig. 1. White blotches and streaks incited by Bacillus megaterium pv. cerealis on field- and glasshouse-grown wheat leaf blades, sheaths, and culms.

injection treatments, caused broad white blotches and narrow white streaks. The blotches caused by the Ps strains were often as broad as those caused by the WB and WBr strains. Plants inoculated with B. megaterium ATCC 14581 and other check treatments developed no blotches. When plants were incubated under high temperature and high light intensity (sodium lamps or intense sunlight), lesions appeared 2-4 days after inoculation. Low temperatures and low light intensities appeared to delay spotting. The pathogens were reisolated from the spots and rarely reisolated from apparently healthy leaves. They were not isolated from check plants.

In three additional trials with airbrush-inoculated L1 and Marquis HRS wheats, strain WBr 14 did not cause spotting. This strain was similar to the other 426 WB and WBr strains and had the same characteristics as the 20 WB and WBr strains (Table 1), except that it did not grow on mannitol.

Swab inoculation of the leaves of white burley tobacco with WB 19, WB 27, WB 148, Ps 488, B. megaterium ATCC 14581, or sterile distilled water did not cause lesion development. However, injection of each of these bacteria into the leaves resulted in chlorotic spots within three days. At 18 days after injection, these spots extended well beyond the initial water-soaked areas of inoculation and had changed to bleached white spots with brown centers. Lesions formed by Ps 488 differed from those of other bacteria in that while still yellow they became filled with brown flecks and then turned white. In one trial, Ps 488 induced spots that turned brown within I day following injection and did not grow beyond the initial soaked areas. The spots resulting from the injection of B. megaterium ATCC 14581 turned chlorotic then white more slowly than those caused by other bacteria. Spots developed from bacteria grown at either 27 or 35 C, with the exception that Ps 488 did not grow at 35 C. Water-injected and untreated plants developed no spots.

The possibility that ozone or sulfur dioxide caused white blotching was eliminated by the absence of air pollution symptoms on *Nicotiana tabacum* L. 'Bel W 3' in the glasshouses.

Additional studies. No vegetative cells or spores of bacteria were found in the cryofractured and critical-point dried lesions.

DISCUSSION

A form of *B. megaterium* (43) causes a white to very light tan blotching and streaking of wheat leaves. The name *Bacillus megaterium* de Bary 1884 pv. cerealis pv. nov. is proposed for this pathovar; the halopathotype strain is WB 28 (8). Strain WB 28 and its strain reisolated via Koch's postulates, WBr 57, will be offered to the American Type Culture Collection, 12301 Parklawn Drive, Rockville, MD 20852.

Bacillus spp. have been reported in association with wheat. B. subtilis increased vigor of wheat in the glasshouse but not in the field (4). It was hypothesized that B. subtilis made minerals available to the plant. B. macerans caused a decay of flax and wheat roots (36), but the decay of flax roots was decreased by using boracic fertilizer (14).

Bacillus megaterium represents a heterogenous group of strains (5,21) found in soil (32,33), roots and tubers (28), stems (17), ovules and seeds (including those of wheat) (31), insects (3), and on uredospores of Puccinia graminis (11). It has been reported to cause proliferation of stem tissue (9), gain in fruit dry matter (41), breakdown of phospho-organic compounds (30), suppression (13,25,45) or promotion (32,33) of other microorganisms, rotting of food storage organs at high temperatures (10), and suppression of smuts in wheat seed (25) and maize seed (13). B. megaterium can survive extreme environmental conditions (2,26).

Yellow to white or light-tan spots and streaks on wheat leaves have been attributed to several causes. Copper deficiency causes a chlorosis and bleaching of leaves in wheat (46). Various viruses cause yellow to whitish streaks and spots on wheat leaves (29,46). Ozone causes white blotching on wheat (22). Sulfur dioxide causes tan-white (46) or ivory (22) leaf blotches on wheat. White to brown leaf streaks and blotches are caused on spring and winter wheats by the bacterium *P. syringae* pv. syringae (34,40,46), which is seed-





Figs. 2-3. Bacillus megaterium pv. cerealis from wheat. 2, Gram stained, showing large ellipsoidal nonstaining spore in some vegetative cells and smaller nonstaining globules in other cells (×1,244). 3, Scanning electron micrograph showing large circular swellings on the vegetative cells (sporangia). One reviewer suggests that these swellings may be "caused by inclusions of poly-B-hydroxybutyrate, as commonly seen in negatively stained preparations" (×1,648).

borne (35). In North Dakota severe white blotches and streaks on wheat are attributable to at least two causes: P. syringae pv. syringae (34) and B. megaterium pv. cerealis. In Canada, leaf spots on wheats called "splotch" (46) were associated with nitrogen deficiency (42) and recognized as distinct from disease caused by P. syringae (46). High temperature and high light intensity greatly increased this disease, whereas 90-100% relative humidity reduced splotchlike disease on Winalta HRW wheat in Alberta in 1965 (1). Winalta is susceptible to white blotch caused by B. megaterium pv. cerealis, and white blotch appears to be enhanced by high temperature and light. Thus, B. megaterium pv. cerealis may have incited the disease in Canada. Lesions, resembling those of white blotch, have been observed in Oklahoma (P. G. Sebesta, personal communication) and Brazil (W. C. da Luz, personal communication). Recent increases in the severity of white blotch symptoms on many cultivars in the field (34,37, and this report) suggest rapid changes towards greater virulence in strains of B. megaterium and/or P. syringae.

Virulence in one strain of *P. syringae*, but not another, was related to a plasmid (38). Whether virulence is related to the presence of a plasmid in the *B. megaterium* pathovars is unknown. Cultures of the *B. megaterium* pathovars grown at 27 and 35 C caused spotting on wheat; the factor(s) causing spotting was not affected by growing the bacterium at 35 C. The large white blotches caused by both bacteria on wheat and tobacco leaves suggest that the pathogenic actions of these bacteria may be similar.

The absence of bacteria in the cryofractured lesions suggested that *B. megaterium* pv. cerealis is present in the host cells in very low numbers; exists outside the cells, but produces a toxin; or that our procedures eliminate the bacterium from the lesions. The bacterium's suppression of other microorganisms (14,25,45) might explain its high rate of recovery from white blotches. The role of detergent in enhancing its recovery is unexplained. Perhaps, the bacterium becomes bound to the host cells and the detergent releases this binding. The often low percentage isolation of other microorganisms from white blotches suggests that something is suppressing the growth of saprophytes in dead tissue.

The relationships between wheat, B. megaterium pv. cerealis, and the environment are relatively unexplored. In general, juvenile (rapidly growing) wheat plants appeared to be resistant to the bacterium. Soft rotting of potato tubers by Erwinia carotovora subsp. atroseptica and Bacillus polymyxa was similarly inhibited by actively growing buds (44). Development of white blotch symptoms by streaking B. megaterium pv. cerealis on leaves suggests that water-soaking of leaf tissues is not necessary for this bacterium to cause disease. In contrast, inoculation procedures that cause water-soaking are necessary for some bacteria to be pathogenic (23). White blotch symptoms often spread through susceptible plantings very rapidly. In the field very susceptible selections such as L1, Froid, and Winoka become severely spotted within 2 days. In one ambiguous development, all 15 B. megaterium pv. cerealis-free L1 headed plants, standing in a common tray of water in an isolated glasshouse with high light intensities and temperatures reaching 28 C, suddenly developed very severe white blotch symptoms. Occasionally white blotch susceptible wheats were severely spotted in several glasshouses during infestations of mites, aphids, and white flies. B. megaterium pv. cerealis was isolated from all the above spots. These and the aforementioned observations suggest that the causal agent of white blotch is spread by water, insects and/or mites, and seed, and that it may be harbored in plant parts, seeds of susceptible cultivars (Table 3) and perhaps in insects. P. syringae pv. syringae is seed transmitted and is epiphytic on wheat leaves (12). B. megaterium pv. cerealis was occasionally isolated from healthy leaves, suggesting that it can be epiphytic.

Attempts to determine field losses from white blotch have not succeeded, due to our inability to prevent severe white blotch in check plots. However, the severity of white blotch at early heading on some field-grown wheat cultivars often equals that of fungus leaf spots that cause economic yield loss (18). Other workers (39) have suggested that bacterial leaf spots of wheat are related to economic crop losses on the basis of yield potentials.

In summary, B. megaterium pv. cerealis causes white blotches and streaks on wheat. The term white blotch is proposed for this disease. The bacterium is also present in leaf spots on oats and barley and in dark streaks on wheat glumes. It is seedborne in small percentages of the seed of susceptible cultivars. It and P. syringae pv. syringae are responsible for an increasing frequency of slight to severe white blotching and streaking of HRS, HRW, and durum wheats in North Dakota. Both bacteria cause broad blotches to narrow lengthwise streaks on wheat leaves. They may differ in that P. syringae pv. syringae causes transient water-soaked streaking, whereas B. megaterium pv. cerealis causes a very broad blotch that covers much of the leaf (Fig. 1).

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