Identification and Origin of *Xanthomonas campestris* pv. *campestris* Races and Related Pathovars

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ABSTRACT

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One hundred sixty-four isolates of *Xanthomonas campestris* pv. *campestris* and other *X. campestris* pathovars known to infect cruciferous hosts (*X. campestris* pvs. *aberrans*, *raphani*, *armoraciae,* and *incanae*) were inoculated onto a differential series of *Brassica* spp. to determine both pathogenicity to brassicas and race. Of these, 144 isolates were identified as *X. campestris* pv. *campestris* and grouped into six races, with races 1 (62%) and 4 (32%) being predominant. Other races were rare. The remaining 20 isolates from brassicas and other cruciferous hosts were either nonpathogenic or very weakly pathogenic on the differential series and could not be race-typed. Five of these isolates, from the ornamental crucifers wallflower (*Cheiranthus cheiri*), stock (*Matthiola incana*) and candytuft (*Iberis* sp.), showed clear evidence of pathovar-like specificity to the hosts of origin. A gene-for-gene model based on the interaction of four avirulence genes in *X. campestris* pv. *campestris* races and four matching resistance genes in the differential hosts is proposed. Knowledge of the race structure and worldwide distribution of races is fundamental to the search for sources of resistance and for the establishment of successful resistance breeding programs.

Additional keywords: black rot of crucifers, disease resistance, pathogen variants.

Black rot of crucifers caused by *Xanthomonas campestris* pv. *campestris* (Pammel) Dowson is possibly the most important disease of crucifers worldwide (35). Economically, the most important host of *X. campestris* pv. *campestris* is *Brassica oleracea* (including cabbage, cauliflower, broccoli, Brussels sprouts, and kale), but it also attacks other *Brassica* spp. and is reported on a number of cruciferous crops, weeds, and ornamentals (3).

The genus *Xanthomonas* has a wide host range extending over 66 genera of nine monocotyledonous families and 160 genera of 49 dicotyledonous families (21). The species *X. campestris* (Pammel) Dowson was formerly divided into 123 pathovars according to host specificity (8). However, recent reclassification of the genus based on DNA-DNA hybridization (31) proposed that the species *X. campestris* should be restricted to *X. campestris* pv. *campestris* and five pathovars that cause disease in cruciferous plants (*X. campestris* pvs. *aberrans* (Knösel) Dye, *armoraciae* (McCulloch) Dye, *barbareae* (Burkholder) Dye, *incanae* (Kendrick & Baker) Dye, and *raphani* (White) Dye. These related pathovars have received little attention, and there have been no extensive comparative studies of their host range. Alvarez et al. (1) and Vauterin et al. (31) expressed some doubt of the distinction of some of these pathovars from *X. campestris* pv. *campestris.*

In addition to distinctions based on host range (pathovars), several *Xanthomonas* spp. and pathovars have been further differentiated into races based on their interaction with differential cultivars. Thus, more than 20 races were proposed for *X. oryzae* (24), 17 races for *X. campestris* pv. *malvacearum* (4,12), and 8 races for *X. campestris* pv. *phaseoli* (25). For *X. campestris* pv. *vesicatoria*, eight races were defined on the basis of their interactions with pepper cultivars and three races with tomato cultivars (16). Kamoun et al. (18) separated the isolates of *X. campestris* pv. *campestris* into five different races (0 to 4) based on the response of certain cultivars of turnip (*B. rapa*) and a cultivar of mustard (*B. juncea*). Other studies indicated that some accessions of *B. napus* and *B. oleracea* have differential reactions to *X. campestris* pv. *campestris* isolates (15). Vicente et al. (33) suggested that race 1 could be subdivided into three races (tentatively designated 1a, 1b, and 1c) on the basis of their reaction on several accessions of *B. oleracea* and one of *B. carinata*. Similarly, Ignatov et al. (14) separated a group of isolates formerly included in race 1 into two races (1 and 5) on the basis of their reaction on two *B. oleracea* accessions.

With the exception of Kamoun et al. (18) and the few recent studies mentioned, all previous studies failed to recognize the existence of races of *X. campestris* pv. *campestris*. Where variation between *X. campestris* pv. *campestris* isolates was recognized, it was generally considered to represent merely a difference in aggressiveness. Most studies of resistance to *X. campestris* pv. *campestris* have been concerned with *B. oleracea,* identifying only a few potentially useful sources (11,36). However, resistance has been found in other *Brassica* spp. (2,10,34). One of the problems in determining the potential usefulness of resistance sources is the misidentification of *Brassica* spp. Flow cytometry and cytology results showed that several accessions were wrongly classified (J. D. Taylor, J. Conway, S. J. Roberts, and J. G. Vicente, *unpublished data*).

This paper presents information on the occurrence of pathogenic variants (races) among isolates of *X. campestris* pv. *campestris* and related pathovars from the United Kingdom and from different geographical regions of the world. An improved differential series for the determination of races of *X. campestris* pv. *campestris* is described. A gene-for-gene model is proposed to explain the interaction of races and differential cultivars. The implications of this model for resistance breeding strategies in *B. oleracea* are discussed.

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MATERIALS AND METHODS

Bacterial isolates. Isolates were obtained in the United Kingdom from field outbreaks of black rot and from commercial seed lots, as part of a number of studies done at Horticulture Research International, Wellesbourne (HRI-W). Isolates were initially considered to be *X. campestris* pv. *campestris* on the basis of colony characteristics on King's medium B (20) or yeast dextrose chalk agar (YDC) and agglutination tests with antiserum conjugated to *Staphylococcus aureus* (22). In addition, representative isolates of *X. campestris* pv. *campestris* and related *X. campestris* pathovars from cruciferous hosts (*X. campestris* pvs. *aberrans*, *armoraciae*, *incanae*, and *raphani*) were obtained from researchers in different countries and from the National Collection of Plant Pathogenic Bacteria (NCPPB). A total of 164 isolates from *Brassica* spp. and other cruciferous species were included in this study (Table 1). Fifteen isolates representative of *Xanthomonas* spp. and pathovars from noncruciferous hosts also were included for comparative purposes. For long-term storage, bacterial growth was suspended in a liquid medium containing 8 g/liter of nutrient broth (Difco Laboratories, Detroit) and 150 ml/liter of glycerol and maintained on glass beads at –76°C (9).

Plant material. The cultivars and accessions used in this study are listed in Table 2. Initially, 12 accessions of *Brassica* spp., including four differentials previously described by Kamoun et al. (18) (Table 3) and other susceptible or differential accessions, were used to characterize the isolates. An improved differential series, including a selection of *Brassica* differentials used previously and three new differentials, was used to further characterize representative isolates of the emerging races (Table 2). At least two plants of each accession were inoculated per isolate. Where accessions were known to lack uniformity (e.g., cv. Seven Top Turnip), at least three plants were used.

The pathogenicity of isolates representative of *X. campestris* pvs. *aberrans*, *armoraciae*, *incanae*, and *raphani*, together with the "race type strains" of the six *X. campestris* pv. *campestris* races, was further tested on two or three plants of Savoy cabbage (*B. oleracea*) cv. Wirosa F1; radish (*Raphanus sativus*) cvs. Mino Early, French Breakfast, and Mantanghong; wallflower (*Cheiranthus cheiri*) cvs. Orange bedder and Primrose bedder; stock (*Matthiola incana*) cv. Brompton stock mixed; and candytuft (*Iberis* sp.) cvs. Hyacinth flowered and Flash mixed. Single plants of horseradish (*Armoracia rusticana*) were inoculated with selected isolates. Pathogenicity of isolates of representative *Xanthomonas* spp. and pathovars from noncruciferous hosts was tested on plants of Savoy cabbage (*B. oleracea*) cv. Wirosa F1 (two plants per isolate).

Plants were raised from seed sown in 9-cm plastic pots filled with Levington M2 compost (The Scotts Company Ltd., Ipswich, UK). Pots were placed in a greenhouse with a minimum temperature of 20/15°C (day/night), venting at 22/17°C (day and night) and with supplementary lighting from October to March to give 16 h days.

Inoculations. Plants were inoculated approximately 4 weeks after sowing. Isolates were grown on King's medium B at 30°C for 48 h before inoculation. Bacterial growth was scraped from the plates and suspended in 10 ml of sterile tap water or saline solution (0.85% NaCl) to produce a turbid suspension (10^8 to 10^9 CFU/ml). Leaves were inoculated by clipping secondary veins, near the margins, with mouse tooth forceps (15). The teeth of the forceps were wrapped in cotton wool to hold inoculum and dipped into the bacterial suspension. Approximately 10 to 12 points of inoculation were made per leaf, and the three youngest leaves on each plant were inoculated. The number of infected points per leaf and the severity of symptoms were assessed 2 and 3 weeks after inoculation. They were rated on a scale of 0 to 3 based on the relative size of the largest lesion on the leaf: 0, no symptoms; 1, slight necrosis or chlorosis surrounding the infection point; 2, typical V-shaped yellow or necrotic lesion with blackened veins with a lesion size of less than 1 cm^2, and 3, typical V-shaped lesion with a size of more than 1 cm^2. Several re-isolations were performed to determine the presence or absence of bacteria in association with disease symptoms in radish, horseradish, and ornamental crucifers.

RESULTS

Pathogenicity of isolates. One hundred forty-four isolates from cruciferous hosts (Table 1) were pathogenic on Savoy cabbage cv. Wirosa F1 and one or more accessions of the *Brassica* spp. tested, giving symptoms generally typical of the disease: V-shaped yellow lesions with black veins and usually with necrotic centers. These isolates were considered to be *X. campestris* pv. *campestris*. Twenty other isolates, including representatives of other pathovars of cruciferous crops (Table 1), were either nonpathogenic or very weakly pathogenic on all the *Brassica* accessions tested. Fifteen isolates representative of *Xanthomonas* spp. and pathovars from noncruciferous hosts (Table 1) failed to produce symptoms after inoculations on cv. Wirosa F1 plants.

Race determination. The reaction of the differential cultivars described by Kamoun et al. (18) (Table 3) was used for the initial separation of *X. campestris* pv. *campestris* isolates into races. Isolates corresponding to Kamoun's races 0, 1, 2, and 4 were identified among those tested, but isolates showing the pattern of reaction of Kamoun's race 3 were not found. In addition, a comparative test of Kamoun's race 3 isolate (HRI 6312) and the "race 4 type strain" (HRI 1279A) was made in paired inoculations on 50 plants of *B. rapa* cv. Seven Top Turnip. Plants were either susceptible to both isolates (7 plants) or resistant to both isolates (43 plants). For this reason, race 3 as defined by Kamoun et al. (18) was withdrawn from our model.

The additional differentials presented in Table 2 were obtained by a process of trial and error as new cultivars or lines with differential responses were identified as part of a screening to identify sources of resistance (Taylor et al., *unpublished data*). We have identified several accessions of *B. oleracea*, e.g., cv. Miracle F1 and a doubled haploid line derived from cv. Böhmerwaldkohl, with resistance to some isolates of race 1. Based on this reaction, race 1 was separated into two races: race 1 (compatible interaction with cv. Miracle F1) and new race 3 (incompatible interaction with cv. Miracle F1). Similarly, a selection from the *B. carinata* accession PI 199947 was susceptible to isolates of race 0 and some isolates of race 1. Based on this reaction, a new race (race 5, compatible interaction with PI 199947) was added to the model. Finally, race 0 was renumbered as race 6 in the new model.

B. rapa cvs. Just Right Turnip and Tokyo Cross Turnip were both uniformly resistant to race 4; Just Right Turnip was selected as the primary race 4 differential. Accessions of *B. napus* cvs. English Giant and Cobra and *B. rapa* cvs. Seven Top Turnip and Green Globe Turnip gave variable reactions when inoculated with several isolates especially from race 4; *B. napus* accession CrGC5 showed variable levels of partial resistance to isolates of this race (Table 2). Of these differentials, only cv. Seven Top Turnip had to be maintained in the new differential series to allow the separation of race 2; a minimum of three plants per isolate was used to allow for variability. The line 14R, a selection from cv. Cobra, was uniformly resistant to race 4 isolates; this line was included as an additional race 4 differential. *B. juncea* cv. Florida Broad Leaf Mustard was fully susceptible only to isolates of race 6, and on this basis was included as a differential. This accession also showed a partially resistant response when inoculated with isolates of race 5. The cabbage accession PI 436606 gave variable reactions when inoculated with isolates of various races (including races 1, 4, and 6) and on this basis was rejected as a potential differential. The broccoli cv. Marathon F1 was susceptible or partially susceptible to isolates of all races, and cv. Wirosa F1 and

TABLE 1. Source and origin of 164 *Xanthomonas campestris* isolates from cruciferous hosts and 15 *Xanthomonas* isolates from noncruciferous hosts

HRI –W isolate (received as)	Source[a] (original designation)	Host	Infected material	Country (region)	Year of isolation
***X. campestris* pv. *campestris* isolates (pathogenic on Savoy cabbage cv. Wirosa F1 and one or more *Brassica* differentials)**					
Race 1					
2309A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1989
3811[b]	P. Williams (PHW1205)	*B. oleracea*		US	
3818A	HRI-W	*B. olerecea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3819A	HRI-W	*Sinapis arvensis*	Leaf	UK (Cornwall)	1994
3843B	A. Ignatov (B19)	*B. oleracea* var. *capitata*	Leaf	Russia (Moscow)	1990
3844B	A. Ignatov (X3)	*B. oleracea* var. *capitata*	Leaf	Russia (Moscow)	1990
3852B	C. Grimm (Xcc750)	*B. oleracea* var. *capitata*	Leaf	Greece	1989
3873	N. Thaveechai (BT7)	*B. oleracea* var. *capitata*	Leaf	Thailand	1982
3874	N. Thaveechai (BT8)	*B. oleracea* var. *capitata*	Leaf	Thailand	1982
3876	NCPPB (1043)	*B. oleracea*		Papua New Guinea	1961
3877	NCPPB (1645)	*B. oleracea* var. *acephala*		Kenya	1964
3965 (*X.campestris* pv. *armoraciae*)	M. Daniels (Xca5)			US	
3966[c]	HRI-W	*B. oleracea*	Leaf	UK (Cornwall)	1995
3971A	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Cornwall)	1995
3972A	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Cornwall)	1995
3973A, 3974A	HRI-W	*Sinapis arvensis*	Leaf	UK (Cornwall)	1995
3975A[c], 3977A[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1995
3976A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1995
5176[c]	HRI-W	*B. oleracea* var. *botrytis*	Seed	UK	1993
5482	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Kent)	1996
5487[c]	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Kent)	1996
5489[c]	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Kent)	1996
5490[c], 5494A[c]	HRI-W	*B. oleracea* var. *sabauda*	Leaf	UK (Kent)	1996
5495[c], 5498[c], 5499[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Kent)	1996
5591[c], 5292[c]	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Seed	UK	1996
5594[c]	HRI-W	*B. oleracea* var. *sabauda*	Seed	UK	1996
5610[c]	HRI-W	*B. oleracea* var. *gemmifera*	Seed	UK	1996
5630[c], 5631[c]	HRI-W	*B. oleracea* var. *botrytis*	Seed	UK (Cornwall)	1996
5714B[c], 5715A[c], 5732[c], 5733[c]	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Lincs)	1996
5734[c], 5735[c], 5736[c], 5739[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Lincs)	1996
5740[c], 5741[c], 5742[c], 5743[c]	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Lincs)	1996
5744[c], 5745[c], 5746[c]	S. Redstone	*B. oleracea* var. *botrytis*	Seed	UK (Cornwall)	1996
5771[c], 5772[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
5773[c], 5778[c], 5779[c], 5780[c], 5782[c], 5783[c], 5784[c], 5789[c], 5791[c]	HRI-W	*B. oleracea* var. *botrytis*	Seed	UK (Cornwall)	1996
5792[c], 5796[c]	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Devon)	1996
5800[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
5802[c]	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Cornwall)	1996
5804[c], 5806[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6018A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6019A[c], 6019C[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6020A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6022A[c]	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Cornwall)	1996
6023A[c], 6024A[c]	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6192	J. Vicente (Xcc562)	*B. oleracea* var. *tronchuda*	Leaf	Portugal (Benavente)	1996
6195	J. Vicente (Xcc565)	*B. oleracea* var. *acephala*	Leaf	Portugal (Lourinhã)	1997
6290	K. Hoenderdal (Xan245)	*B. oleracea* var. *capitata*			1972
6381	NCPPB (529)	*B. oleracea* var. *capitata*		UK	1957
6413	D. Silué (1869)	*B. oleracea* var. *botrytis*		France	1997
6414	D. Silué (4)	*B. oleracea* var. *botrytis*		France	1997
7283	HRI-W	Cruciferous weed	Leaf	UK (Cornwall)	1997
7286	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1997
7292	HRI-W	Cruciferous weed	Leaf	UK (Cornwall)	1997
7657	HRI-W	*B. oleracea* var. *botrytis*	Debris	UK (Cornwall)	1998
7804	K. Serfontein (BD64)	*B. oleracea* var. *capitata*		South Africa (Brits)	1997
7805	K. Serfontein (BD102)	*B. oleracea* var. *botrytis*	Leaf	South Africa (Marble Hall)	1998
7807	K. Serfontein (BD116)	*B. oleracea* var. *capitata*	Seed	South Africa	1998
7809	K. Serfontein (BD140)	*B. oleracea* var. *capitata*	Leaf	Namibia (Caprivi Strip)	1999
7810	K. Serfontein (BD152)	*B. oleracea* var. *botrytis*	Stem	South Africa (Marble Hall)	1999
Race 2					
3849A[b]	C.I. Kado (2D520)	*B. oleracea* var. *botrytis*	Seed	US	
Race 3: included in race 1 of Kamoun et al. (18)					
3851A	C. Grimm (Xcc168)	*B. oleracea* var. *botrytis*	Leaf	Greece	1989
5212[b]	NCPPB (528)	*B. oleracea* var. *gemmifera*		UK	1957
6412	D. Silué (1713)	*B. oleracea* var. *botrytis*		France	1997
Race 4					
738C	HRI-W	*B. oleracea* var. *botrytis*	Pod	US	1973
1279A[b]	HRI-W	*B. oleracea* var. *capitata*	Leaf	UK (Cornwall)	1984

(*continued on next page*)

[a] HRI-W, Horticulture Research International, Wellesbourne, UK; NCPPB, National Collection of Plant Pathogenic Bacteria, Sand Hutton, UK.
[b] Proposed race type strains.
[c] Isolates not tested on the three new differentials (Miracle F1, PI 199947 and Cobra 14R); these isolates are most probably race 1.

TABLE 1. (*continued from preceding page*)

HRI –W isolate(received as)	Source[a] (original designation)	Host	Infected material	Country (region)	Year of isolation
2243A	HRI-W	*Brassica* sp.		Kenya	1988
3820A, 3830A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3831A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3832A, 3833A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3834A, 3835A	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3836E	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3964	M. Daniels (147)			Brazil	
5190	HRI-W	*B. oleracea* var. *botrytis*	Seed	UK	1993
5485	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Kent)	1995
5486	HRI-W	*B. olerecea* var. *gemmifera*	Leaf	UK (Kent)	1996
5582, 5585, 5586, 5587, 5588, 5589	HRI-W	*B. oleracea* var. *botrytis*	Seed	UK	1996
5651, 5655	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
5659, 5661	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Devon)	1996
5737	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Lincs)	1996
5808, 5811A, 5811B, 5812, 5814, 5816, 5819	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1996
6189	J. Vicente (Xcc559)	*B. oleracea* var. *italica*	Leaf	Portugal (Muge)	1996
6194	J. Vicente (Xcc564)	*B. oleracea* var. *capitata*	Leaf	Portugal (Lourinhã)	1997
6309A	HRI-W	*B. oleracea*	Leaf	Spain	1998
6312	C.I. Kado (2D513R)	*B. oleracea* var. *botrytis*	Leaf	US (California)	
6366	M. Scortichini (053)	*B. oleracea* var. *gongylodes*	Leaf	Italy (Latina)	1994
6367	M. Scortichini (352)	*B. oleracea* var. *botrytis*	Leaf	Italy (Latina)	1991
6368	V. Catara (62.4)	*B. oleracea* var. *gongylodes*	Leaf	Italy	1996
6369	V. Catara (65.3)	*B. oleracea* var. *italica*	Leaf	Italy	1996
7290	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1997
7758	HRI-W	*B. oleracea* var. *tronchuda*	Leaf	Brazil (Minas Gerais)	1999
7803	K. Serfontein (BD63)	*B. oleracea* var. *capitata*		South Africa (Brits)	1997
7806	K. Serfontein (BD105)	*B. oleracea* var. *capitata*	Leaf	South Africa (Northam)	1998
7808	K. Serfontein (BD128)	*B. oleracea* var. *capitata*	Stem	South Africa	1999
Race 5: included in race 1 of Kamoun et al. (18)					
3880[b] (*X. campestris* pv. *aberrans*)	NCPPB (2986)	*B. oleracea* var. *capitata*		Australia	1975
3883 (*X. campestris* pv. *raphani*)	NCPPB (1946)	*Raphanus sativus*		US	1966
6382	NCPPB (1711)	*B. rapa*		Canada	1953
Race 6: race 0 of Kamoun et al. (18)					
6181[c]	J. Vicente (Xcc551)	*B. rapa*	Leaf	Portugal (Sardoal)	1996
6185	J. Vicente (Xcc555)	*B. rapa*	Leaf	Portugal (Castelo Branco)	1996
Wake or nonpathogenic on Savoy cv. Wirosa F1 and on *Brassica* differentials					
3777A	HRI-W	*Cheiranthus cheiri*	Leaf	UK	1994
3836C	HRI-W	*B. oleracea* var. *botrytis*	Leaf	UK (Cornwall)	1994
3842B	A. Ignatov (PA1)	*B. oleracea* var. *capitata*		Russia (Moscow)	1993
3845B	A. Ignatov (13-56)	*B. oleracea* var. *capitata*		Germany	1988
3846B	A. Ignatov (Xc8181)	*B. oleracea* var. *capitata*		Russia (St. Petersburg)	1990
3875	A. Franken (Xcc102)	*B. oleracea* var. *capitata*			
3961	M. Daniels (8004)	*B. oleracea* var. *botrytis*		UK	1958
3962	M. Daniels (8417)			UK	
3963	M. Daniels (8480)			UK	
5219	NCPPB (2517)	*Cheiranthus cheri*		UK	1973
5713A	HRI-W	*B. oleracea* var. *capitata* × *sabauda*	Leaf	UK (Lincs)	1996
5790	S. Redstone (19-1-1.1)	*B. oleracea* var. *botrytis*		UK (Cornwall)	1996
6374 (*X. campestris* pv. *aberrans*)	NCPPB (875)	*B. oleracea* var. *botrytis*		Germany	1958
6375 (*X. campestris* pv. *armoraciae*)	NCPPB (347)	*Iberis* sp.		Tanzania	1954
6376 (*X. campestris* pv. *armoraciae*)	NCPPB (1930)	*Amoracia rusticana*			1939
6377 (*X. campestris* pv. *incanae*)	NCPPB (937)	*Matthiola* sp.		US	1950
6378 (*X. campestris* pv. *incanae*)	NCPPB (1934)	*Matthiola incana*		US	1949
6379	NCPPB (45)	*B. napus*		UK	1941
6380	NCPPB (404)	*B. napobrassica*		New Zealand	1953
6383	NCPPB (2857)	*B. napus*		UK	1975
***Xanthomonas* isolates from noncruciferous hosts (not pathogenic on Savoy cabbage cv. Wirosa F1)**					
64A	HRI-W	Lobelia	Leaf	UK	1967
1944E (*X. campestris* pv. *phaseoli*)	HRI-W	*Phaseolus vulgaris*		Rwanda	1987
2134B	HRI-W	*Allium cepa*	Leaf	Barbados	1988
2376A	HRI-W	*Allium cepa*	Leaf	Barbados	1989
3243A (*X. campestris* pv. *vitians*)	HRI-W	*Latuca sativa*	Leaf	Portugal	1992
3342A (*X. campestris* pv. *phaseoli*)	A.F. Opio (1002)	*Phaseolus vulgaris*		Uganda	1993
3416A (*X. campestris* pv. *phaseoli*)	HRI-W	*Phaseolus vulgaris*		Tanzania	1993
3872E (*X. campestris* pv. *vitians*)	HRI-W	*Latuca sativa*	Leaf	Kenya	1995
5232 (*X. campestris* pv. *malvacearum*)	NCPPB 633[b]	*Gossypium* sp.		Sudan	1958
5235 (*X. campestris* pv. *vesicatoria*)	NCPPB 422[b]	*Lycopersicum esculentum*		New Zealand	1955
5616 (*X. campestris* pv. *pelargonii*)	HRI-W	Pelargonium	Leaf	UK	1996
5852 (*X. hortorum* pv. *hedera*)	HRI-W	*Hedera hibernica*	Leaf	UK	1997
6013 (*X. fragariae*)	M. Scortichini (030)	*Fragaria* × *ananassa*	Leaf	Italy (Latina)	1993
6014 (*X. campestris* pv. *pruni*)	M. Scortichini (006)	*Prunus salicina*	Leaf	Italy (Latina)	1991
6301 (*X. campestris* pv. *carotae*)	NCPPB (3440)	*Daucus carota*		Brazil	1985

B. napus cv. Capricorn were susceptible to all the races. Cultivar Wirosa F1 was preferred as the "susceptible control" (susceptible to all isolates and races).

Occurrence and distribution of races. According to the classification of Kamoun et al. (18) (Table 3), isolates from the United Kingdom belonged to race 1 (70%) and race 4 (30%) (Table 4). All isolates of the original race 1 that were tested on the new differential series were confirmed as the new race 1 with the exception of the NCPPB type strain (NCPPB 528; HRI 5212), which was reclassified as the new race 3. Due to the very low frequency of race 3, UK isolates that were not fully tested on the new differential series were most likely to conform to the new race 1 designation (Table 4). Races 2, 5, and 6 were not found among any UK isolates.

Race 1 of Kamoun et al. (18) was also predominant among isolates outside the United Kingdom (57%), followed by race 4 (36%) (Table 5). All original race 1 isolates from non-UK sources were tested on the new differential series. These isolates were mainly confirmed as the new race 1, but two European isolates (from Greece and France) were identified as new race 3, and three non-European isolates (from Australia, Canada, and the United States) were identified as new race 5. Overall, races 2, 3, 5, and 6 were rare among the non-UK isolates tested.

There appeared to be no relationship between race and geographical origin of the isolates, but some evidence for a relationship between race and host of origin was found. Race 1, 2, 3, and 4 isolates were all from different *B. oleracea* crops or cruciferous weeds growing in association with *B. oleracea* crops (Table 1). However, four of the five isolates that comprised races 5 and 6 were from turnip (three isolates) or radish (one isolate, received as *X. campestris* pv. *raphani*). The single isolate of race 5 from *B. oleracea* was received as *X. campestris* pv. *aberrans*. Moreover, the isolates of races 5 and 6 often produced lesions with extensive dark necrosis and only limited chlorosis (blight-like symptoms) on susceptible hosts such as cv. Wirosa F1.

***X. campestris* pathovars.** The results of inoculations of other cruciferous species including known hosts of related pathovars are presented in Table 6. Representative isolates of the six *X. campestris* pv. *campestris* races were pathogenic on radish, but not on horseradish. There was no evidence of good compatible interactions between the *X. campestris* pv. *campestris* isolates and wallflower, stock, and candytuft cultivars, but small atypical lesions were occasionally observed. Radish cultivars gave variable reactions with isolates of races 2, 3, and 5. Generally, the isolate of race 2 was only weakly pathogenic even on cv. Wirosa F1, and gave variable responses on radish and wallflower. Two of the race 5 isolates, 3880 and 3883 (previously included in pvs. *aberrans* and *raphani*), probably are not sufficiently distinct from *X. campestris* pv. *campestris* to warrant the status of distinct pathovars.

X. campestris isolates from wallflower, stock, and candytuft showed clear evidence of specificity to their host of origin. These isolates were not aggressive on the *X. campestris* pv. *campestris* susceptible control cv. Wirosa F1. Isolates from wallflower were aggressive on wallflower, but nonpathogenic or weakly pathogenic on other ornamental species. Isolates from stock were very aggressive on stock causing systemic infections and defoliation. The single isolate from candytuft was the only aggressive isolate on candytuft. The isolate from horseradish was only very weakly pathogenic on its host, causing some small lesions and darkening of veins, and nonpathogenic on other hosts.

New differential series and gene-for-gene model. The improved differential series is shown in Table 7, together with a postulated gene-for-gene model to explain the relationship between races and cultivars. Several hypotheses for the allocation of paired resistance (R) and avirulence (A) genes were considered. The model presented is the simplest hypothesis involving the smallest number of genes (four gene pairs) necessary to explain the observed interactions. In this hypothesis, where the pattern of reaction of differential accessions was similar, gene homology was assumed but not tested. A more complex model would be necessary if the differentials Just Right Turnip, Cobra line 14R, and Seven Top Turnip have different genes conferring resistance to race 4, and if PI 199947 and Florida Broad Leaf Mustard have different genes conferring resistance to race 1.

DISCUSSION

Races. The identification of races within *X. campestris* pv. *campestris* by Kamoun et al. (18) (Table 3) was confirmed in the

TABLE 3. Initial differentiation of *Xanthomonas campestris* pv. *campestris* into five races[a]

Differential cultivars	Races				
	0	1	2	3	4
Wirosa F1 (*Brassica oleracea*)	+	+	+	+	+
Just Right Hybrid Turnip, Tokyo Cross Hybrid Turnip (*Brassica rapa*)	+	+	+	–	–
Seven Top Turnip (*Brassica rapa*)	+	+	–	+	–
Florida Broad Leaf Mustard (*Brassica juncea*)	+	–	+	–	–

[a] Adapted from Kamoun et al. (18); + compatible interaction (susceptibility); – indicates incompatible interaction (resistance).

TABLE 2. *Brassica* spp. accessions used for race typing the isolates

Cultivar or accession	Species / variety	Type	Origin	Reaction
Used in initial assays				
Wirosa F1[a]	*B. oleracea* var. *sabauda*	Hybrid	Bejo Zaden NV., Netherlands	Susceptible (control)
Marathon F1	*B. oleracea* var. *italica*	Hybrid	E.W. King & Co. Ltd, UK	Susceptible
PI 436606	*B. oleracea* var. *capitata*	Open pollinated	USDA; ex. China	Variable partial resistance to races 1, 2, 3, 5, 6
Green Globe Turnip (HRI 3437)	*B. rapa* var. *rapifera*	Open pollinated	HRI Genetic Resources Unit, UK	Variable resistance to race 4
Just Right Hybrid Turnip[a]	*B. rapa* var. *rapifera*	Hybrid	Otis S. Twilley Seed Co., US	Resistance to race 4
Tokyo Cross Hybrid Turnip	*B. rapa* var. *rapifera*	Hybrid	Otis S. Twilley Seed Co., US	Resistance to race 4
Seven Top Turnip[a]	*B. rapa* var. *rapifera*	Open pollinated	Otis S. Twilley Seed Co., US	Resistance to race 2; variable resistance to race 4
Florida Broad Leaf Mustard[a]	*B. juncea*	Open pollinated	Otis S. Twilley Seed Co., US	Resistance to races 1, 3, and 4
CrGC5 (rapid cycling)	*B. napus* var. *rapifera*	Open pollinated	Crucifer Genetics Cooperative, US	Partial resistance to race 4
Cobra (oilseed rape)	*B. napus* var. *oleifera*	Open pollinated	Twyfords, UK	Variable resistance to race 4
English Giant (fodder rape)	*B. napus* var. *oleifera*	Open pollinated	Charles Sharpe and Company, UK	Variable resistance to race 4
Capricorn (oilseed rape)	*B. napus* var. *oleifera*	Open pollinated	Plant Breeding Institute, UK	Susceptible
Added to the differential series				
Miracle F1[a]	*B. oleracea* var. *botrytis*	Hybrid	Bejo Zaden NV., Netherlands	Resistance to race 3
Selection of PI 199947[a]	*B. carinata*	Open pollinated	USDA; ex. Ethiopia	Resistance to races 1, 3, and 4
Line 14R of Cobra[a]	*B. napus* var. *oleifera*	Self pollinated	This study	Resistance to race 4

[a] Accessions included in the new differential series.

present study with the exception of race 3. The differentiation of Kamoun's races 3 and 4 depended on the reaction of *B. rapa* cv. Seven Top Turnip. So far, we have found no isolate that conforms to the expected differential reactions of this race. The single isolate (2D513; HRI 6312A) used by Kamoun et al. (18) gave a similar response to an isolate of race 4 in our tests. These tests also showed that cv. Seven Top Turnip was a genetic mixture giving variable reactions to race 4. Therefore, the uncertainty over the separation of race 3 may have been due to the variable response of cv. Seven Top Turnip. The designation of three races of Kamoun et al. (18) was retained (races 1, 2, and 4) in the new model. Race 0 was redesignated as race 6. This change in designation was mainly to avoid the implication that race 0 isolates, which were pathogenic to all *Brassica* accessions in the differential series, lacked avirulence genes. As this cannot be proven, and because we have recently identified *Brassica* accessions resistant to this race (J. D. Taylor et al., *unpublished data*), it was considered advisable to avoid the "race 0" designation.

Our results indicate that the original race 1 of Kamoun et al. (18) can be divided into at least three races (1, 3, and 5) based on the reactions of two *B. oleracea* accessions (cv. Miracle F1 and a doubled haploid line derived from cv. Böhmerwaldkohl) and an accession of *B. carinata* (PI 199947). Kamoun et al. (18) commented on the considerable variation in virulence among isolates they designated as race 1. Ignatov et al. (14) separated race 1 isolates into two races, which they designated 1 and 5. Race 3 in our model (a rare race) probably corresponded to Ignatov's race 1. We decided to reserve the race 1 designation for the most common race. Thus the NCPPB type strain of *X. campestris* pv. *campestris* was included in race 3. Other authors have noted that this strain caused blight symptoms (1,6) and in this respect is not typical of the majority of *X. campestris* pv. *campestris* isolates. In our experience blight-like symptoms (dark necrotic lesions with limited chlorosis) were more common in *B. oleracea* accessions inoculated with isolates of races 5 and 6. The ability to elicit blight symptoms may be under genetic control (6), but may also be influenced by environmental conditions, especially temperature. Two isolates classified in this study as race 5 of *X. campestris* pv. *campestris* were the NCPPB type strains of *X. campestris* pv. *aberrans* and *X. campestris* pv. *raphani*. Since these isolates show only small pathogenic differences from other *X. campestris* pv. *campestris* isolates, their original pathovar status may be unwarranted. Vauterin et al. (31) questioned the relevance of these two pathovar designations. The single isolate that represents race 2 (HRI 3849A) appears to differ from all other isolates of *X. campestris* pv. *campestris*. This isolate has been used extensively in molecular studies of resistance in *Arabidopsis thaliana* (5,17, 29). It is unfortunate that important studies have been made with an isolate that appears to be both atypical and rare.

Distribution of races. Race 1 appears to be currently the most common race in *B. oleracea* crops in the United Kingdom. Worldwide, races 1 and 4 are predominant. Races 2, 3, 5, and 6 were rare in the collection tested. Race 2 and race 6 (previously designated race 0) were also absent in a collection of isolates from Japan and Russia (13). The low frequency of race 3 may be due to the extensive use of cultivars that are resistant to this race (J. D. Taylor et al., unpublished data). This may not always have been the case, since the NCPPB type strain of *X. campestris* pv. *campestris*, isolated in 1957, is race 3. Race 5 was not found among European isolates. Race 6 was not found among UK isolates, but this may have been due to the preponderance of isolates from *B. oleracea*. In Portugal, race 6 is common in turnip (32). Monitoring the frequency and distribution of races worldwide is essential to the development of effective strategies for resistance breeding.

The three isolates from cruciferous weeds that were examined in this study were of the same race as present in associated *B. oleracea* crops. It is suggested that the infection originated from the crops, because the crops frequently showed uniform infections and the weeds were sparse. Smith (28) also considered that the cultivated plants were more likely to be a source of inoculum for weeds than vice versa. Dane and Shaw (7) observed that the dispersal of a marked strain of *X. campestris* pv. *campestris* from cabbages to weeds was frequent.

Pathovars. A pathovar is defined as "a strain or set of strains with the same or similar characteristics, differentiated at the infrasubspecific level from other strains of the same species or subspecies on the basis of distinctive pathogenicity to one or more plant hosts" (8). On the basis of host specificity, the isolates examined in this study appear to represent four distinct pathovars of *X. campestris*. Most of the *X. campestris* pv. *campestris* isolates obtained in this study were pathogenic to a number of *Brassica* accessions, including cv. Wirosa F1, confirming their identification as *X. campestris* pv. *campestris*. The only isolates that were clearly different from *X. campestris* pv. *campestris* in respect of host range were those that had originated from wallflower, stock, and candytuft. Of the recognized names, only *X. campestris* pv. *incanae* appears to be appropriate for the isolates that are pathogenic on stock. Our results are in agreement with the descriptions of Kendrick (19) and Wilson (37). The isolates from wallflower should not be included in *X. campestris* pv. *incanae* as suggested by Bradbury (3), nor in *X. campestris* pv. *campestris*, because they were clearly specific in their pathogenicity to wallflower and were not pathogenic on the differential series of *Brassica* spp. A single isolate from candytuft listed as *X. campestris* pv. *armoraciae* was pathogenic to candytuft but not to horse-

TABLE 4. Frequency of occurrence and host of origin of *Xanthomonas campestris* pv. *campestris* races among 102 UK isolates

Race designation			
This study	Kamoun et al. (18)	Host of origin (number of isolates)	Isolates
1	1	*Brassica oleracea* var. *botrytis* (40)	70[a]
		Brassica oleracea var. *capitata* × *sabauda* (14)	
		Brassica oleracea var. *sabauda* (3)	
		Brassica oleracea var. *capitata* (6)	
		Brassica oleracea var. *gemmifera* (1)	
		Brassica oleracea var. unknown (1)	
		Sinapis arvensis and other weeds (5)	
3	1	*Brassica oleracea* var. *gemmifera* (1)	1
4	4	*Brassica oleracea* var. *botrytis* (28)	31
		Brassica oleracea var. *capitata* × *sabauda* (1)	
		Brassica oleracea var. *capitata* (1)	
		Brassica oleracea var. *gemmifera* (1)	

[a] Thirty-eight of these isolates were not tested on the three new differentials (Miracle F1, PI 199947, and Cobra 14R); these isolates are most probably race 1.

TABLE 5. Frequency of occurrence and geographical distribution of *Xanthomonas campestris* pv. *campestris* races among 42 non-UK isolates

Race designation			
This study	Kamoun et al. (18)	Country of origin (number of isolates)	Isolates
1	1	France (2), Greece (1), Kenya (1), Namibia (1), Papua New Guinea (1), Portugal (2), Russia (2), South Africa (4), Thailand (2), US (2), unknown (1)	19
2	2	US (1)	1
3	1	Greece (1), France (1)	2
4	4	Brazil (2), Italy (4), Kenya (1), Portugal (2), South Africa (3), Spain (1) , US (2)	15
5	1	Australia (1), Canada (1), US (1)	3
6	0	Portugal (2)	2

radish. These isolates from wallflower and candytuft are clearly distinct in their host range and may warrant the creation of new pathovars. *X. campestris* pv. *armoraciae* was described as the causal agent of a nonvascular leaf spot disease of horseradish (23). Later, leaf spots on cauliflower, cabbage, turnip, and radish were also attributed to this pathovar (6,26,27). One isolate received under this pathovar designation caused symptoms of *X. campestris* pv. *campestris* in some of the *Brassica* differentials and had probably been misidentified. The single isolate from horseradish tested gave only a weakly pathogenic reaction on horseradish. We did not observe leaf spots in our tests, but the inoculation method used (leaf clipping) might not be the most appropriate for symptom development. Spray inoculating might be a better method to produce leaf spots. We were unable to substantiate or refute the existence of *X. campestris* pv. *armoraciae*.

Some of the isolates that were either nonpathogenic or very weakly pathogenic had been obtained from other researchers and official collections. Neither the pathovar nor the race of these isolates could be determined. Loss of pathogenicity may have been due to poor maintenance conditions, and preserving isolates in an appropriate way is important for their long-term survival.

Differential series and gene-for-gene model. A modified and improved differential series was established in this study. This series has some disadvantages: it includes some cultivars, such as cv. Seven Top Turnip, which give variable reactions and were shown to be genetic mixtures. It also includes F1 hybrids that give uniform reactions, but their availability is problematic, depending on their commercial success. It is important, therefore, that the differential series is improved through the development of uniform lines, either through several generations of self-pollination or preferably through microspore or anther culture. If uniform lines of differential cultivars were maintained in a germplasm bank, their availability for research and for resistance breeding would be ensured.

The proposed gene-for-gene model shown in Table 7 is based on the interaction of at least four matching gene pairs. The genes that confer resistance to the most important races (1 and 4) were designated R1 and R4. The gene R1, present in *B. carinata* accession PI 199947 and possibly in *B. juncea* cv. Florida Broad Leaf Mustard, confers resistance to races 1 and 3 (with A1) and possibly to race 4 if this race also has A1. This gene could have originated in the B genome of *B. nigra* from which these two species are derived. The reaction of *B. rapa* cv. Just Right Turnip and *B. napus* cv. Cobra line 14R is explained by the interaction of R4 with the avirulence gene A4 present in race 4. This gene could have originated in the A genome of *B. rapa*. R2, present in *B. rapa* cv. Seven Top Turnip, confers resistance to the single isolate of race 2. R3, present in *B. oleracea* cv. Miracle F1, confers resistance to race 3 and possibly to races 2 and 5, which have A3. Cultivar Florida Broad Leaf Mustard might have another gene that could explain the partial resistance to isolates of race 5. The model allows for the possible inclusion of additional gene pairs if new races and differentials are identified. In general, the model was constructed in a way that reflects the origin of the allotetraploid species of *Brassica* (30): R1 originates from the B genome, R3 from the C genome, and R4 from the A genome.

The postulated gene-for-gene relationship provides a basis for understanding the interactions of races and cultivars, but to be

TABLE 6. Host range of *Xanthomonas campestris* pathovars from cruciferous hosts[a]

HRI isolate	Original designation	Host of origin	Pathogenicity to[b]					
			Savoy cabbage	Radish	Wallflower	Stock	Candytuft	Horseradish
3811 (1)	*X. campestris* pv. *campestris*	*B. oleracea*	+	+	–	–	–	–
3849A (2)	*X. campestris* pv. *campestris*	*B. oleracea*	+	+/–	+/–	–	–	–
5212 (3)	*X. campestris* pv. *campestris*	*B. oleracea*	+	+/–	–	–	–	–
1279A (4)	*X. campestris* pv. *campestris*	*B. oleracea*	+	+	–	–	–	–
6382 (5)	*X. campestris* pv. *campestris*	*B. rapa*	+	+/–	–	–	–	nt
6181 (6)	*X. campestris* pv. *campestris*	*B. rapa*	+	+	–	–	–	–
3880 (5)	*X. campestris* pv. *aberrans*	*B. oleracea*	+	+/–	–	–	–	–
3883 (5)	*X. campestris* pv. *raphani*	*Raphanus sativus*	+	+/–	–	–	–	nt
3777A, 5219A	*X. campestris* pv. *campestris*	*Cheiranthus cheiri*	–	–	+	–	–	nt
6377, 6378	*X. campestris* pv. *incanae*	*Matthiola* sp.	–	–	–	+	–	nt
6375	*X. campestris* pv. *armoraciae*	*Iberis* sp.	–	+/–	–	–	+	–
6376	*X. campestris* pv. *armoraciae*	*Armoracia rusticana*	–	–	–	–	–	(+)

[a] +, compatible interaction (susceptibility); –, incompatible interaction (resistance); (+), weakly pathogenic; +/–, variable reaction between and within cultivars; nt, not tested.

[b] Savoy cabbage, *Brassica* oleracea); radish, *Raphanus sativus*; wallflower, *Cheiranthus chieri*; candytuft, *Iberis* sp.; stock, *Matthiola incana*; and horseradish, *Armoracia rusticana*.

TABLE 7. Postulated gene-for-gene model to explain the relationship between *Brassica* cultivars and races of *Xanthomonas campestris* pv. *campestris*[a]

Differential cultivars or accessions	Resistance genes					Races/Avirulence genes (A)					
						1	2	3	4	5	6
						A1	…	A1	A1?	…	…
						…	A2	…	…	…	…
						…	A3	A3	…	A3	…
						…	…	…	A4	…	…
						…	…	…	…	…	…
						…	…	…	…	?	…
Wirosa F1 (*B. oleracea*)	…	…	…	…	…	+	+	+	+	+	+
Just Right Hybrid Turnip (*B. rapa*), Line 14R of Cobra (*B. napus*)	…	…	…	R4	…	+	+	+	–	+	+
Seven Top Turnip (*B. rapa*)	…	R2	…	R4	…	+	–	+	–	+	+
PI 199947 (*B. carinata*)	R1	…	…	R4?	…	–	+	–	–	+	+
Florida Broad Leaf Mustard (*B. juncea)*	R1	…	…	R4?	?	–	+	–	–	(+)	+
Miracle F1 (*B. oleracea)*	…	…	R3	…	…	+	–	–	+	–	+

[a] + = compatible interaction (susceptibility); – = incompatible interaction (resistance); and (+) = weakly pathogenic.

fully validated the model needs to be supported by genetic and molecular data from both the host and the pathogen. In the case of the host, results of crosses made recently to establish the inheritance of resistance to some of the races indicate that R1, R3, and R4 are single dominant genes (J. G. Vicente, J. G. Taylor, D. J. Lydiate, I. A. P. Parkin, A. G. Sharpe, and G. J. King, *unpublished data*).

The model, and more especially the availability, of defined race type strains should assist in the selection of resistant material for breeding programs. Disease resistance screening must be done with isolates representing the full pathogenic variation of *X. campestris* pv. *campestris* and especially the major races, 1 and 4. In addition, isolates of race 6 can be used to detect potential race-nonspecific resistance. Future breeding programs aiming to achieve durable resistance will need to combine race-specific resistance genes (R1 and R4) that confer strong resistance to the most important races of the pathogen. If possible, they will also need race-nonspecific genes that could confer quantitative resistance to all known races.

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