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Race-specific reaction of resistance to black rot in *Brassica oleracea*

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Abstract

Several black rot-resistant varieties of *Brassica oleracea* showed a race-specific hypersensitive response (HR) to inoculation with *Xanthomonas campestris* pv. *campestris* isolates of different races. In progenies of cabbage line PI436606, Portuguese kale ISA454 and Chinese kale SR1 the HR to race 1 of the pathogen was controlled by a dominant gene named R1, when a recessive gene r5 was responsible for the HR to race 5. Genes with a similar race-specific reaction were assumed on the basis of gene-for-gene interaction in black rot-resistant Japanese cabbage cultivars and double haploid lines obtained from them. Homology of gene r5 in cabbage lines PI436606, Fujiwase 01 and kale ISA454 was postulated in crosses between those lines or their progenies. In a cross between SR1 and PI436606, interaction between resistance to race 1 and non-specific resistance localized in the stem vascular system was found. On the basis of pedigree information and homology of resistance genes in the cultivars of East-Asian cabbage and Portuguese kales, the probable origin of race-specific resistance to black rot of cole crops was suggested to be in heading Mediterranean kale. Some evidence was found for a gene conferring resistance to race 4 in *B. oleracea*.

Introduction

Black rot of brassicas is a damaging disease with a world-wide distribution caused by *Xanthomonas campestris* pv. *campestris* (Xcc). Kamoun et al. (1992) grouped a limited number of isolates of Xcc into five races according to the response of different cultivars of *Brassica rapa* and *B. juncea*. In a further study, race-specific resistance was found in many other varieties of *B. rapa* and in *B. napus* (Ignatov et al., 1997). However, breeding of *B. oleracea* for resistance is usually undertaken without recognition of the existence of pathogenic races.

The purpose of the present research was to clarify whether any distinctive race-specific reaction of resistance exists in cultivars of *B. oleracea.*

Materials and methods

Seeds of differentials for Xcc races (Kamoun et al., 1992), cultivars and doubled haploid (DH) lines of cabbage resistant to black rot (Table 1) were obtained from the collection of the Vegetable Breeding Department, NIVOT, Japan. Rapid cycling kale CrGC3.4 and cabbage line Badger Inbred 16 were obtained from Crucifer Genetics Cooperative, University of Wisconsin-Madison, USA. Cabbage line PI436606 was kindly provided by Professor M.H. Dickson, Cornell University, USA. Two accessions of Portuguese Penca kale ISA55 and ISA454, resistant to black rot, (Ferreira et al., 1993) were kindly provided by Professor J.C.S. Dias, Lisbon University, Portugal.

Inbred Chinese kale line SR1, with nonrace-specific resistance to black rot localized in the plant stem and controlled by the major dominant gene Rs, and partial resistance to race 1 (A. Ignatov, unpubl.), was produced by 4 cycles of self-pollination from the

Table 1. Brassica oleracea accessions grouped according to their postulated resistance genes

Subspecies	Accession	R genes
alboglabra	Chinese kale SR1	R1
tronchuda	Penca kale ISA55, ISA454	R1, R5
capitata	Badger Inbred 16, Kinkei DH01, Reiho DH01, Fujiwase 01; Fujiwase DH01, 02, 05; Harukei DH01	R1, R5
	PI436606; DH M9606; Aichi dai Bansei DH01,02	R5
	Reiho DH01, 03; Fujiwase DH03,04	R5, R4
	DH M9603; M9604	R4

Chinese kale SR1, cabbage PI436606, Badger Inbred 16 and Fujiwase 01 are inbred lines; Penca kales ISA55, ISA454 are single plant selections with uniform resistance reaction; DH are doubled haploid lines, obtained from the corresponding cultivars. The resistance gene 4 was assumed based on gene-for-gene interaction with *Xanthomonas campestris* pv. *campestris* race 4.

line CrGC3.4. A single plant of SR1 was then crossed with cabbage line PI436606. The F_1 plants were vernalized for 9 weeks at 5 °C, and then bud pollinated to generate F_2 and BC_1. The F_1, BC_1, and F_2 from crosses between Portuguese kale ISA454, resistant to races 1 and 5, and kale lines CrGC3.4 and SR1 were obtained through bud pollination. Plants of PI436606 and Fujiwase 01, and those selected from ISA454 or their progenies (Table 5) were inter-crossed to test homogeneity of the postulated resistance genes.

All plants were grown in a greenhouse in 8 cm Jiffy pots (Denmark), containing granulated artificial soil, and supplied every week with the complete mineral fertilizer Hyponex (USA).

The type strain of Xcc NCPPB528 was obtained from the National Collection of Plant Pathogenic Bacteria (UK), as a representative for race 1. Isolate PHW117 was obtained from the Crucifer Genetic Cooperative, University of Wisconsin-Madison, USA. The isolates Xn1, Xn2 and Xn5 were collected from diseased broccoli plants in Ano, Mie prefecture, Japan, during 1996–1997. The isolates of Xcc belonged to races 4 (Xn1) and 1 (Xn4, PHW117 and Xn5), according to the reaction of the differentials in preliminary tests. The isolates were maintained on YDS (yeast, dextrose, calcium carbonate agar) slants at 4 °C. For inoculation, a 36 h culture of bacteria was grown on plates with King's B medium at 28 °C. Bacteria were scraped from the surface of the cultures with spatula and suspended in phosphate buffer pH 7.0 to obtain a suspension approximately 10^6 CFU/ml.

For evaluation of the leaf hypersensitive response (HR) plants 4-weeks or more were inoculated by clipping the edges of the leaves near veins in 2–3 mm from leaf border with mouse-tooth forceps dipped in a suspension of Xcc. About 10 points of inoculation were made per leaf. Every plant was tested with isolates of three races. Absence of any interaction between races in the case of simultaneous inoculation was established in preliminary experiments. After inoculation, the plants were kept in glasshouse at a temperature of about 28 °C/18 °C day/night under 16 h light day. Initial symptoms appeared 10 days after inoculation, and in 16 days plans were rated on the basis of disease progress. Plants with localized necrotic (hypersensitive) reaction or with a few (1–3) small lesions (less than 3 mm) near inoculation points were rated as resistant. Plants with V-shape lesions from 10 to 50 mm in lenghth, developed from most of inoculation points were described as susceptible. If it was impossible to rate a plant as definitely resistant or susceptible, the F_3 family was produced and tested. No quantitative difference in symptoms among susceptible plants was estimated by such rating.

An excised cotyledon assay (Alvarez et al., 1994) was applied to test the stem reaction. The disease progress was evaluated at 6 and 16 days. Highly susceptible plants had a black vein extending from the point of inoculation and V-shaped lesions on the leaves. Stem-resistant plants had no symptoms.

Most of the F_1, BC_1 and F_2 families were evaluated for segregation of resistance in three independent experiments. Some populations with a limited amount of seeds were inoculated two times on younger leaves to confirm the reaction. No significant acquired resistance was observed if subsequent inoculation was done at 4-week intervals.

Table 2. Postulated pairs of avirulence – resistance genes in interaction between resistant brassicas and isolates of *Xanthomonas campestris* pv. *campestris*

Brassica species	Accession	Resistance gene	Reaction with race/avirulence gene				
			Race 1/A1		Race 4/A4	Race 5/A5	
			NCPPB 528	Xn4	Xn31	PHW 117	Xn5
B. rapa	Just Right (F_1)	R4	+	+	−	+	+
B. rapa	Tokyo Cross (F_1)	R4	+	+	−	+	+
B. rapa	Seven Top Green	R4	+	+	−	+	+
B. juncea	Florida Broad Leaf	na	−	−	−	−	−
B. oleracea	CrGC3.4	none	+	+	+	+	+
B. oleracea	Badger Inbred 16	R1, R5	−	−	+	−	−
B. oleracea	ISA 454	R1, R5	−	−	+	−	−
B. oleracea	SR1	R1	−	−	+	+	+
B. oleracea	PI436606	R5	+	+	+	−	−
B. oleracea	F_1 SR1 × PI436606	na	−	−	+	+	+
B. oleracea	F_1 SR1 × ISA454	na	−	−	+	+	+
B. oleracea	F_1 CrGC3.4 × ISA454	na	−	−	+	+	+

+: Susceptible, −: Hypersensitive response (HR), na: Not applicable.
The resistance and avirulence genes were postulated based on the assumed gene-for-gene interaction between resistant varieties of brassicas and isolates of the pathogen. For genetic uniformity, a single plant selection was obtained from open pollinated varieties.

The probability (P) of expected gene segregation in F_2 and BC_1 populations was estimated on the basis of chi-squared test.

Results

Race designation

The isolates of Xcc PHW117, NCPPB528, Xn5 and Xn4 were identified as race 1 on the differentials of Kamoun et al. (1992) (Table 2). Despite that, the isolates Xn5 and PHW117, and the type strain of race 1 NCPPB528 possessed clearly distinctive reaction on *B. oleracea* line PI436606 and kale SR1 (Table 2). For purposes of resistance analysis in the present study, a new race 5 represented by isolates Xn5 and PHW117 was proposed on the basis of that reaction.

Pattern of gene-for-gene interaction

The cabbage lines Badger Inbred 16, Fujiwase 01 and DH lines obtained from Japanese cabbage cultivars Fujiwase, Reiho No 1, Kinkei 201, Harukei and selections from the Penca kale accessions ISA55 and ISA454 had resistance to both races 1 and 5. Lines PI436606, DH M9606, Aichi Daibansei DH01 and 02 were resistant only to race 5. The Chinese kale line SR1 had partial resistance to race 1, expressed as restricted lesions that developed from 1 or 2 points of inoculation, and full susceptibility to race 5 (Tables 1, 2).

On the assumption of a gene-for-gene interaction between *B. oleracea* cultivars and races of Xcc, two matching gene pairs of avirulence (A1 and A5) in pathogen isolates and resistance (R1 and R5) in these accessions were postulated (Table 2).

Lines Badger Inbred 16, Fujiwase 01 and others resistant to races 1 and 5 appear to have both genes of specific resistance R1 and R5, whereas PI436606 and others resistant to race 5 only had only gene R5. The partially resistant kale line SR1 appeared to have only the gene R1.

Avirulence genes A1 and A5 were assumed to be present in the isolates of races 1 and 5. The avirulence gene A4 in race 4 (Table 2) was proposed on the basis of its interaction with the matching dominant gene of resistance R4 in *B. rapa* differentials Just Right (F_1) and Seven Top Green (A. Ignatov, unpubl.).

Genetic analysis of resistance

All F_1 plants obtained in crosses between the kale lines SR1 and CrGC3.4 and accession ISA454 of Penca kale were resistant to race 1. The ratio of segregation in the F_2 population of the CrGC3.4 × ISA454 cross was close to 3 resistant:1 susceptible, and no segregation was found in the F_2 of SR1 × ISA454. The reaction

Table 3. Segregation in progenies of resistant varieties against 3 races of *Xanthomonas campestris* pv. *campestris* (1st experiment)

Progeny	Race	Segregation (expected number)		Total	Resistance gene (ratio)	P >
		resistant	susceptible			
F_2SR1 × PI436606 (1)	1	93 (92)	71 (72)	164	R1Rs (9:7)	0.9
	5	43 (41)	121 (123)	164	r5 (1:3)	0.75
	4	1 (0)	163 (164)	164	none	na
F_2SR1 × PI436606 (2)	1	19 (20)	16 (15)	35	R1R2 (9:7)	0.8
	5	44 (44)	130 (130)	174	r5 (1:3)	0.99
	4	2 (0)	172 (174)	174	none	na
BC_1 F_1(SR1 × PI436606) (1) × SR1	1	52 (52)	0 (0)	52	R1 (1:0)	na
	5	0 (0)	52 (52)	52	none	na
	4	0 (0)	52 (52)	52	none	na
F_2SR1 × ISA454	1	151 (151)	0 (0)	151	R1 (1:0)	na
	5	42 (40)	118 (120)	160	r5 (1:3)	0.5
	4	0 (0)	160 (160	160	none	na
BC_1 F_1 (SR1 × ISA454) × SR1	1	28 (28)	0 (0)	28	R1 (1:0)	na
	5	0 (0)	28 (28)	28	none	na
	4	0 (0)	28 (28)	28	none	na
F_2CrGC3.4 × ISA454	1	128 (126)	40 (42)	168	R1 (3:1)	0.5
	5	45 (42)	123 (126)	168	r5 (1:3)	0.5
	5	0 (0)	168 (168)	168	none	na
BC_1F_1 (CrGC3.4 × ISA454) × CrGC3.4	1	29 (27)	25 (27)	54	R1 (1:1)	0.5
	5	0 (0)	54 (54)	54	none	na
	4	0 (0)	54 (54)	54	none	na
BC_1F_1 (CrGC3.4 × ISA454) × ISA454	1	42 (42)	0 (0)	R1 (1:0)	na	
	5	22 (21)	20 (21)	42	r5 (1:1)	0.5
	4	0 (0)	42 (42)	42	none	na

Na: Not applicable.

of BC_1 obtained for the cross CrGC3.4 × ISA454 also favored a single dominant gene of resistance (Table 3).

The F_2 populations obtained from the two F_1 plants of cross SR1 × PI436606 were evaluated against isolate of race 1, and expression of resistance was found to be considerably higher than in the parent line SR1. The ratio of resistant to susceptible plants was close to 9:7 (Table 3). A participation of two dominant genes with additive interaction might be expected in such a case. When the F_2 plants were divided into stem-resistant and stem-susceptible sub-populations, these showed different segregations against race 1. In the stem-resistant bulk, the segregation was close to that expected for a dominant gene (3:1). In the stem-susceptible bulk, only two plants were rated resistant to race 1 (Table 4), but their F_3 families were still susceptible (data not shown). Thus, it is likely that the resistance to race 1 in this population has been expressed only in plants with stem resistance found previously in parent line SR1.

It was assumed that both the Portuguese kale ISA454 and the kale SR1 possessed the dominant gene named R1, which conferred HR on race 1. The homology of R1 gene in these plants was confirmed by the lack of segregation in F_2 and BC_1 populations (Tables 2 and 3).

All plants of BC_1 (F_1 (SR1 × PI436606) × SR1), obtained from the first F_1 parental plant were susceptible to race 5 and resistant to race 1. The F_2 populations obtained from crosses SR1 × PI436606, SR1 × ISA454 and CrGC3.4 × ISA454 showed segregation against the isolate of race 5 that was explained by the action of a single recessive gene. Reaction of BC_1 plants obtained for the progeny of SR1 × ISA454 confirmed this possibility. This gene, designated in Tables 1 and 2 as R5, was further called r5 (Table 3).

Table 4. Segregation of race-specific reaction among the stem-resistant and stem-susceptible plants in F_2(SR1 × PI436606) (1) (2^{nd} and 3^{rd} experiment)

Group of stem reaction	Segregation of leaf reaction (expected numbers) to:					
	Race 1		Ratio/P >	Race 5		Ratio/P >
	R	S		R	S	
2^{nd} experiment						
R (Rs^+)	202 (203)	68 (67)	3:1/09	66 (68)	204 (203)	1:3/0.9
S (Rs^-Rs^-	1 (0)	90 (91)	na	19 (22)	72 (68)	1:3/0.5
Total	203 (203)	158 (158)	9:7/0.9	85 (90)	276 (271)	1:3/0.5
3^{rd} experiment						
R (Rs^+	90 (92)	33 (31)	3:1/0.7	28 (31)	96 (93)	1:3/0.5
S (Rs^-Rs^-)	1 (0)	42 (41)	na	10 (11)	33 (32)	1:3/0.9
Total	91 (92)	74 (72)	9:7/0.9	38 (42)	129 (125)	1:3/0.5

R: Resistant, S: Susceptible plants for leaf or stem reaction, na: Not applicable.

Table 5. Test of homology of the postulated resistance gene r5

Population	Segregation		Total (ratio)	P >
	R	S		
P1436606 × Fujiwase 01, F_1	36	0	36	na
PI436660 × ISA454, F_1	48	0	48	na
F_1(CrGC3.4 × ISA454) × Fujiwase 01	16 (17)	18 (17)	34 (1:1)	0.75
F_1(CrGC3.4 × ISA454) × PI1436606	29 (31)	33 (31)	62 (1:1)	0.5
F_1 (SR1 × PI436606) × F_1 (SR1 × ISA445)	16 (16)	48 (48)	64 (1:3)	0.99

R: resistant (hypersensitive response), S: Susceptible, na: Not applicable, expected number of plants in every class given in brackets.

The F_1 plants obtained from the crosses between line PI436606 and Fujiwase 01, PI436606 and the selection from ISA454, all homozygous for the r5 gene, showed no segregation in reaction to race 5. Plants obtained from the cross between F_1 (CrGC3.4 × ISA454), heterozygous for r5, and Fujiwase 01 showed 1:1 segregation against race 5. The population obtained from the cross between F_1 (SR1 × PI436606) and F_1 (CrGC3.4 × ISA454) segregated with a ratio close to 1 resistant:3 susceptible (Table 5). Thus, the r5 gene in cabbage and Penca kale seems to be homologous. Resistance to race 1 in all these populations segregated independently from resistance to race 5, indicating that these two loci are located in different linkage groups (data not shown).

Most of the tested plants of the parents, F_1, F_2 and BC_1 populations were completely susceptible to race 4. However, some DH lines obtained from black rot-resistant Japanese cultivars showed stable HR to the isolate of race 4, even though they were susceptible to races 1 and 5, and gene R4 was suspected in such a case (Table 2). We intend to investigate this reaction in a further study.

Discussion

Since the first report of black rot-resistant cabbage cultivars (Bain, 1952; Bain, 1955), resistance has been detected in other *B. oleracea* accessions (Table 3). A number of studies have confirmed the oligogenic and additive nature of resistance to black rot in *B. oleracea* (Camargo et al., 1995; Dickson and Hunter, 1987; Williams et al., 1972). Plant defense includes several biochemical events, and participation of several genes in the phenotypic expression of resistance can be expected. Two cabbage cultivars, Fujiwase from Japan and Hei Ye Da Ping Tou (PI436606) from China, have been used to introduce resistance into commercial varieties. The black rot resistance of plants selected from the variety Fujiwase was conferred by a major recessive gene (Williams et al., 1972), as well as the resistance from line PI436606 (Dickson and Hunter, 1987). Unfortunately, these genes showed complex relationships with other genes in different crosses. Recently, using mapping of quantitative trait loci (QTL), the resistance in Fujiwase progeny was found to be associated with several additive loci in different linkage groups. One locus was responsible for resistance in both adult and young stages and was recessive whereas the other was dominant (Camargo et al., 1995). Midvein inoculation was applied in that study, although the expression of the resistance genes was associated with leaf HR (Staub and Williams, 1972).

In the present study, the resistant accessions of *B. oleracea* and their segregating progeny expressed a race-specific interaction with Xcc races 1, 4 and 5. The method of inoculation applied here provided clearer differentiation between resistant and susceptible reactions compared with other methods, because the wounds made by the mouse-tooth forceps were more uniform, as was the amount of inoculum placed at every inoculation point, and the area of inoculation at the leave edges was narrow near hydathodes, where expression of resistance is stronger than in the case of inoculation in veins (Staub and Williams, 1972). Since the response of veins and hydathodes to inoculation was distinctive, race-specific resistance seems to be expressed mainly in leaf mesophyll tissues.

The method of symptom rating applied here did not estimate the additive interaction between the resistance genes, expected from previous studies (Camargo et al., 1995; Williams et al., 1972), except for the interaction of R1 gene with stem resistance. Although designation of resistance genes in cabbage varieties (Table 1) solely on the assumption of gene- for-gene interaction is tentative, it should not be ruled out that at least some of the resistant phenotypes found in *B. oleracea* suggest a race-specific expression, and that were vigorous genetic analysis could identify the genes involved.

Perhaps, part of the variation of resistance explained by the quantitative loci found in *B. oleracea* (Camargo et al., 1995) could be higher if other methods of inoculation in a glasshouse were applied.

Several cabbage DH lines and Fujiwase 01, have displayed a pattern of race-specific reaction against Xcc races 1 and 5 similar to that of Penca kale (Table 1). Dickson and Hunter (1987) previously found that the recessive gene from PI436606 had no interaction with gene(s) from Badger Inbred 16. However, only seedlings were tested, and it was especially emphasized that resistance of Badger Inbred 16 was not expressed at that stage, being explained by lack of the gene responsible for resistance at young age in Fujiwase (Bain, 1955; Camargo et al., 1995; Hunter et al., 1987). The use of genetic markers in analysis of race-specific HR could more clearly determine whether the genes proposed in the present experiments are the same as those that other researchers have studied.

Cabbages were introduced to Japan at the beginning of 20th century and most of them had ancestral varieties of the Flat Dutch group (Shinohara, 1959). This group was selected from a heading Mediterranean kale related to the landrace Penca de Mirandella (Lizgunova, 1984), which is also resistant to black rot (Ferreira et al., 1993). As tested by Bain (1952), cabbage varieties related to Flat Dutch had a high frequency of resistant plants in bulk. In the same experiments resistance in the Fujiwase was demonstrated, applying inoculum of similar race composition. Since Fujiwase has a documented origin from Flat Dutch (Shinohara, 1959), and Hei Ye Da Ping Tou belongs to this group as well (Lizgunova, 1984), it is highly probable that the assumed homologous genes of resistance were inherited from heading Mediterranean kale.

This idea, that the race-specific resistance to black rot in Asian cabbages did not appear under pressure of the disease, as suggested by some researchers (Williams et al., 1972), but was probably inherited from plants related to heading Portuguese kales is a new one.

Since the race structure of Xcc populations varies considerably between countries with large areas under brassicas (Ignatov et al., 1997; Vicente et al., 1997; A. Ignatov, unpubl.) plant breeding for resistance to black rot should be undertaken with comprehensive knowledge of the pattern of race-specific resistance and race structure of local populations of the pathogen.

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