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Identification of Cladosporium fulvum Cooke races from group B and C on tomatoes in Poland

B. LESKI

Institute of Plant Protection, Warsaw Agicultural University, Poland

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Abstract

Further races of *Cladosporium fulvum* Cooke were identified on tomatoes in Poland: one race of group B affecting the resistance gene Cf-4 (similar to the hypothetic race 1.4) and 2 races from group C affecting the gene combination Cf-2 Cf-4 (one resembling the Dutch race 2.3.4. and the other to the hypothetic race 1.2.3.4). A list of varieties susceptible and resistant to these races is given.

INTRODUCTION

At the beginning of the previous decade a dozen or so varieties of tomatoes were imported to Poland, showing different resistance to *Cladosporium fulvum*. In the first years of cultivation two single races (1 and 3) constituting an admixture of the natural fungus population and later a new race not known at the time (L e s k i 1967, 1970a) were discovered.

The variety V-548 introduced into the Polish selection list continues to be cropped beside the F_1 hybrid varieties imported from Holland. We still have to date no original home variety of glasshouse tomatoes.

In the breeding programme, conducted since 1964 in the Department of Plant Pathology Warsaw Agricultural University with the application of Canadian material resistant to *C. fulvum*, more than a dozen promising breeding lines and F_1 tomato hybrids were selected (also resistant to *Verticilium* spp. and the tabacco mosaic virus). The resistant material was tested on a commercial scale in the neighbouring glasshouse complex Mysiadło where they remained immune from *C. fulvum* up to the period 1973-1975. From this date on the appearance of single *C. fulvum* lesions on some breeding lines and varieties was noted there and in other glasshouses. The appearance of new *C. fulvum* races (although with very low incidence) has greatly disturbed our up-to-date

efforts and obliges us to introduce essential changes in our breeding programme.

The present paper reports on the identification of new physiological *C. fulvum* races and the reaction of some varieties of tomatoes to them.

LITERATURE REVIEW

Cladosporium fulvum Cooke is one the commonest and most dangerous tomato pathogens in regions where they are cultivated as greenhouse crops. In spite of the high effectiveness of systemic fungicides, in countries where greenhouse gardening is highly advanced immune varieties (also to some other diseases) are exclusively cultivated. Breeding of varieties resistant to *C. fulvum* has been conducted for more than 50 years. Beginning with the thirties many varieties were bred, mainly in Canada, in which the dominant major genes for resistance were derived from the variety "Stirling Castle" (Cf-1) and related species, *Lycopersicon pimpinellifolium* (Jusl.) Mill. (Cf-2, Cf-3), and Cf-4, from the green-fruiting species of the subgenus *Eriopersicon* (Langford 1937; Bayley 1947; Kerr 1957; 1959; Guba 1956; Kerr and Bayley 1964).

The progress in breeding of resistant varieties was accompanied from the beginning by physiological specialization of the pathogen. Subsequent races appeared frequently in a relatively short time as new varieties were introduced for cultivation. Up to 1950 only group A of races with specific virulence towards the first 3 resistance genes was known (Langford 1937; Bayley 1950). Among the races which could be differentiated by the use of these genes, race 1.3 was not found know until 1973, (Stamova and Jordanov 1973). With the spread of resistant tomato cultivation, part of these races appeared at various times in other countries (Day 1954; Termohlen 1960; Kishi 1962; Ghabrial and Pirone 1963; Leski 1967, 1970a; Levkina 1968; Betlach and Havrankova 1973). On most of these tomato varieties a small number of races occurs, usually simple, breaking the effect of single genes. Leski (1967, 1970) demonstrated that two simple races (1 and 3) occurred in Poland in several regions in small quantity in natural fungus populations before any varieties resistant to *C. fulvum* were introduced. Day (1967) proved the mutational origin of the *C. fulvum* races by obtaining a high frequency of induced mutations of races 0 to 2. A historical review of this period of investigations is given by Persiel (1967).

Hopes of a lasting solution of the problem of fungus races were attached to the breeding of a series of varieties to which the simultaneous presence of 4 resistance genes was ascribed (Kerr 1955; 1957,

1957a, 1959, 1963). These varieties (among them Vagabond, V-548 and Vantage) were cultivated in Canada and several other countries and used as a source of resistance genes for F_1 hybrids and in further breeding in Holland and G. Britain (Kooistra 1964). These varieties in most countries continue to be immune.

In 1964 new races of group B appeared in Holland (Kooistra 1964; Hubbelin 1966) and further races of group were C identified 3 years later (Hubbeling 1971). At about the same time there appeared in Canada race 10 breaking the resistance based on the single gene Cf-4 (Bayley and Kerr 1964) and then the races 11 and 12 (Patrick, Kerr and Bayley 1971). Race 12 resembles the Dutch 2.3.4. race, whereas the characteristic of race 11 does not fit the race system based on the gene-for-gene hypothesis of Flor (1965). Both these races (11 and 12) are virulent towards Cf-2 and Cf-4 and they may be classified to group C. In 1965 there appeared in Poland on the breeding lines a race virulent to the Cf-4 (Leski 1970, 1970a) which was not identified at the time.

Lately in breeding of new varieties a gene Cf-5 of resistance to all the so far described fungus races is used (Patrick, Kerr and Bayley 1971) and several other resistance genes have been identified (Lenhardt and Kerr 1972). The canadian authors whose studies are the foundation of nearly all successful breeding along this line, continue to number the *C. fulvum* races in the order in which they are detected, without any schematic classification. Day (1965), on the basis of the gene-for-gene hypothesis (Flor 1956) and Person's model (1959), introduced a system linking the nomenclature system of *C. fulvum* races with the numbering of the resistance genes in test varieties. The classification of races into groups A, B and C (Hubbeling 1966) is very practical and may be reliably performed with the use of genes Cf-2 and Cf-4.

Recently Boukema and Garretsen (1975) demonstrated that a high general resistance level — "horizontal" according to Robinson (1959) — is attached to the gene Cf-1. The level of this resistanse is, however, variable and so far does not seem useful in practice.

MATERIAL AND METHODS

In the present paper which is actually a continuation of earlier studies, methods not differing from those already described were applied (Leski 1967, 1970a).

Part of the *Cladosporium fulvum* strains which broke the resistance effect of the single gene Cf-4 the variety Purdue-135 had been isolated

Table 1

Developped system of *Cladosporium fulvum* Cooke races with proved or forecasted reactions with test genotypes of tomatoes, based on "gene-for-gene" system

Differential set of gene-testers in test-tomatoes	Group A								Group B				Group C				
	According to: Bayley 1950; Bayley, Kerr 1964; Patrick, Kerr, Bayley 1971																
	1	2	5	9	8	—	7	6	10	—	—	—	11	—	—	12	—
	According to: Day 1956; Termohlen 1960; Hubbeling 1968, 1971																
	0	1	2	3	1.2	1.3	2.3	1.2.3	4	1.4	3.4	1.3.4.	?	2.4	1.2.4	2.3.4	1.2.3.4
	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Cf-1	R	S	R	R	S	S	R	S	R	S	R	S	R	R	S	R	S
Cf-2	I	I	S	I	S	I	S	S	I	I	I	I	S	S	S	S	S
Cf-3	R	R	R	S	R	S	S	S	R	R	S	S	S	R	R	S	S
Cf-4	I	I	I	I	I	I	I	I	S	S	S	S	R	S	S	S	S
Cf-1 Cf-2	R	I	R	I	S	I	R	S	I	I	I	I		R	S	R	S
Cf-1 Cf-3	R	R	R	I	R	S	R	S	I	I	I	S		R	R	R	S
Cf-2 Cf-3	I	I	R	I	R	I	S	S	I	I	I	I		R	R	S	S
(Cf-1 Cf-4)	I	I	I	I	I	I	I	I	R	R	R	R		R	S	R	S
Cf-2 Cf-4	I	I	I	I	I	I	I	I	I	I	I	I	R	S	S	S	S
(Cf-3 Cf-4) *	I	I	I	I	I	I	I	I	S	R	S	S		R	R	S	S
Cf-1 Cf-2 Cf-3	I	I	R	I	R	I	R	S	I	I	I	I		R	R	R	S
(Cf-1 Cf-2 Cf-4) *	I	I	I	I	I	I	I	I	I	I	I	I		R	S	R	S
(Cf-1 Cf-3 Cf-4) *	I	I	I	I	I	I	I	I	R	R	R	S		R	R	R	S
(Cf-2 Cf-3 Cf-4) *	I	I	I	I	I	I	I	I	I	I	I	I		R	R	S	S
(Cf-1 Cf-2 Cf-3 Cf-4) *	I	I	I	I	I	I	I	I	I	I	I	I		R	R	R	S
Cf-5	I	I	I	I	I	I	I	I	I	I	I	I		I	I	I	I

I — immune; R — resistant; S — susceptible.

* Gene sets not represented by availlable varieties; can be obtained in F_1 crosses between respective genotypes.

as early as 1965-1967. They had been tested repeatedly at various times, in order to reveal their interaction mainly with genes Cf-1 and Cf-3.

The remaining strains were isolated from typical lesions appearing at various times on resistant tomatoes, mainly in the glasshouses of the Mysiadło complex near Warsaw, where ontinuous observations of resistant varieties and breeding lines were carried on, as well as in the complexes in Niemce near Lublin, Naramowice near Poznań and some other glasshouses in the environs of Warsaw. As fungus strains were sampled, preliminary tests were started on a restricted set of varieties differentiating the race A, B and C groups. In order to increase the chance of detection of possibly all the races, high inoculum concentrations ($2\text{-}5\times10^6$) were used in preliminary tests, containing a mixture of strains of similar origin (variety, locality), and its nonhomogenicity was revealed, they were separated and spores were reisolated from single lesions for further tests. From strains preliminary identified within the group of races one-spore cultures were prepared (by the dilution method) for final identification.

Series of infections were done in experimental glasshouses as a rule under natural light in the spring (March-April) and autumn (Sept.--Oct.) periods.

Inoculum was usually prepared from two weeks old cultures of the fungus on PDA medium with glucouse added. The resistance of the collection of available varieties and breeding lines was tested with the identified races.

For infection 3-8-leaf tomato plants were used growing in pots (ϕ 10-14 cm) on peat-moss soil in conditions favouring vigrous growth. In each test one strain or one group were inoculated on a dozen or so plants of each variety. After inoculation (spraying of both leaf surface with inoculum) a 100 per cent RH was maintained for 24-48 h, and later ca 80 per cent RH at a temperature of 17-25°C. Only those test results were taken into account in which typical and distinct disease symptoms appeared not later than after 4 weeks on the standard susceptible variety (Potentat, Starfire). At later periods secondary cross infestation may occur.

The infection spectrum of the tested strains was established and compared with that of known or hypothetical races from table 1 which serves as key for races, taking into account the natural differentiation of the phenotypic effects of the particular genes or the expected host-pathogen (H-P) interrelationships. A sufficiently reliable identification can be achieved with the use of a part of these gene combinations.

Table 2

Comparison between races of *Cladosporium fulvum* Cooke of group B

Test plants	Resistance genes	Race 10 (Bayley Kerr 1964)	Race 4 (Hubbeling 1968, 1971)	Polish strains			Remarkcs referring to differences
				Mixture of 16 strains (spring tests)	Strains 1 and 2 (spring tests)	Strains 1 and 2 (autumn tests)	
1	2	3	4	5	6	7	8
Potentat	—	S	S	S	S	S	
LMR-1		—	R	S−	S	S	
Stirling Castle	Cf-1	R+	R	R	R	R−	×
Antimold-A		R	R	R	R	R−	
Vetemold	Cf-2	I	I	I	I	I	
Antimold-B		R	—	—	—	—	
V-121	Cf-3	R+	R	R	R−	R−	
V-473, Vulcan		I	I	I	I	I	
Vetomold ×LMR-1	Cf-1 Cf-2	—	—	I	I	I	
L. pimpinellifolium Vineland V-469	Cf-2 Cf-3	I	I	I	I	I	
59-R			I	R	R	R−	
V-121×LMR-1	Cf-1 Cf-3		—	R−	R−	R−	×
V-473×V-121		—	—	I	I	I	
F-101	Cf-1 Cf-2 Cf-3	R+	I	R	R	R−	×
L. pimpinellifolium P.I. 112215		I		I	I	I	

[1981]

1	2	3	4	5	6	7	8
Purdue-135	Cf-4	S	S	S	S	S	
P-135×LMR-1				S−	S−	S	
P-135×St. Castle	Cf-1 Cf-4			R−	R−	S−	
P-135×V-121	Cf-3 Cf-4			R−	R	R−	
P-135×V-473	Cf-1 Cf-2 Cf-4			I	I	I	
P-135×V-469	Cf-2 Cf-3 Cf-4			I	I	I	
Vinequeen, V-548, Vagabond	Cf-2 Cf-4	I	I	I	I	I	
Vantage		R	I	I	I	I	×
Improved Bay State		I		R	R	R	×
WMPF-22		R+		R+	R+	R	
WMPF-54		S		S−	S−	S	
V-542, V-596		R	I	I	I	I	×

I: immune, R: resistant, S: susceptible; R−: lowered level of resistance; S−: lovered level of susceptibility; R+: higher level of resistance (only yellow spots).

COURSE AND RESULTS OF EXPERIMENTS

From the crosses done since 1963 between the series of Canadian varieties resistant to *C. fulvum* and early varieties resistant to other diseases, breeding lines were selected and tested in commercial conditions in the glasshouses of the Gardening Complex at Mysiadło near Warsaw. At the same time a collection of resistant and test varieties for *C. fulvum* races was cultivated in these glasshouses. In the autumn of 1965 there appeared traces of a new race breaking the resistance of the varieties WMPF-54 and Purdue-56. The infection spectrum for this race (beside races 0, 1, 3) has been described without final identification (Leski 1967, 1970). Soon part of the breeding material, the resistance of which was derived among others from the varieties V-548, Vagabond and Vantage which remained resistant, became slightly diseased. In 1968 lesions were also found on the variety Eurocross BB. All the isolates proved identical with the earlier ones and were specifically virulent towards the single gene Cf-4. The infection spectrum for 2 strains (one from Eurocross BB and another from the breeding lines) and for the mixture of 16 identical isolates of this race on an extended test material is compiled in Table 2. It gives at the same time a comparison with other races of group B. Test experiments with strains of this race were carried out in various conditions (spring, autumn), in order to ascertain their action towards varieties with gene Cf-1 and Cf-3.

Since Stirling Castle used by Canadian breeders is to some extent resistant (LMR-1 is not) to races 12 and 10, and for differentiation of races in group B the effect of gene Cf-1 (in LMR-1) should be taken into account, the isolated race can only be denoted as 1.4.

The wide use for cropping of immune varieties practically eliminated the disease for some time from glasshouses, so that only very slight symptoms were noted on the test variety. Potentat in 3 commercial glasshouses. In the autumn of 1972 sporadical lesions were found on plants of the breeding lines and further single spots also in other glasshouses and plastic tunnels on the varieties V-548, Rewermun, Virase and Pagham Cross. Several lesions were found in 1975 on plants of the latest Dutch hybrid varieties in Naramowice and Niemce.

As more isolates of the fungus were sampled, series of tests were performed with single isolates or their mixtures. Totally 36 fungus isolates were tested. In only 3 cases was an admixture of a race of group B noted. The remaining isolates belonged to group C races.

A number of one-spore cultures were derived from strains selected by reisolation from plants with genes Cf-2 and Cf-4 (Vagabond, V-548). These were tested in a series of infection experiments at various dates on an extended differentialtest set. The infection spectrum established

Table 3

Comparison of *Cladosporium fulvum* Cooke races of group C

Test plants	Resistance genes	Race 11 (Patrick, Kerr, Bayley 1971)	Race 12 (Patrick, Kerr, Bayley 1971)	Race 1. 2. 4 (Hubbeling 1971)	Race 2. 3. 4 (Hubbeling 1971)	Polish strains N-3, N-4 (2.3.4)	Polish strains J-2 (2.3.4)	Polish strains M-2, M-6 (1.2.3.4) (spring tests)	Polish strains M-2, M-6 (1,2,3,4) (autumn tests)
Potentat	—	S	S	S	S	S	S	S	S
LMR-1		S—	R—	S	R	R—	R—	S	S
Stirling Castle	Cf-1	R	R	S	R	R	R	S	S
Antimold A			**R**			R	R	S	S
Vetomold	Cf-2	S	S	S	S	S	S	S	S
V-121	Cf-3	S	S	R—	S	S	S	S	S
Purdue-135	Cf-4	R	S	S	S	S	S	S	S
V-473	Cf-1 Cf-2			S	R—	R—	R—	S	S
V-469						S	S	S	S
L. pimpinellifolium (Vineland)	Cf-2 Cf-3			R—	S	S	S	S	S
59-R (Hol.)	Cf-1 Cf-3					R—	R—	S	S
L. pimpinellifolium P.I. 112215	Cf-1 Cf-2 Cf-3					R—	R—	S—	S
F-101				R—	R—	R—	R—	S—	S
Vantage				S	S	S	S	S	S
Vendor						S	S	S	S
V-548	Cf-2 Cf-4					S	S	S	S
Vinequeen		R	S	S	S	S	S	S	S
Vagabond				S	S	S	S	**S**	**S**
WMPF-54						S	S	S	S

R: resistance (relative); R—: lower level of relative resistance; S: susceptibility; S—: higher level of susceptibility.

in these tests for representative isolates (one-spore strains) is shown in Table 3 in comparison with other races of this group. These strains were primarily isolated from crops at Mysiadło (M-2 from V-548, M-6 from Virase), at Jabłonna (J-2 from Revermun) and at Naramowice (N-3 from Revermun, N-4 — variety unknown).

In the autumn of 1975, 10-14 plants of each new breeding line nad various varieties were infected with a mixture of strains from group C. The following varieties were found to be susceptible: Vendor, V-548, Vagabond and our breeding lines selected from crosses with these varieties as well as F_1 crosses of Duth origin — Revermun, Eurocross BB, Panase, Fabiola, Nebu II, Virase, Milores. The newest Dutch F_1 hybrids Jet, Extase and Cura proved resistant.

IDENTIFIED RACES OF *C. FULVUM*

In spite of some minor differences between races described in Holland and Canada the home strains of *Cladosporium fulvum* differentiated in this study can be classified according to the scheme proposed by Hubbeling (1971).

Race 1.4 like other races of group B and race 10 (Canadian) is specifically virulent to the Cf-4 gene. It is also virulent towards Cf-1 in the variety LMR-1, whereas the varieties Stirling Castle and Antimold A are relatively resistant to this race. Since Stirling Castle is also resistant to race 12 (though LMR-1 is susceptible) this variety must posses some other factor beside the gene Cf-1. Other differences between the races are shown in Table. 2.

1.2.3.4 is, like the races of group C, specifically virulent towards the set of genes Cf-2 and Cf-4. Moreover, varieties with single genes Cf-1 or Cf-3 are distinctly susceptible.

The F-101 variety resistant (R) to Dutch races of this group (1.2.4 and 2.3.4) is distinctly susceptible to 1.2.3.4. In repeated test conducted at different dates it was possible to distinguish the reaction of the variety F-101 to this race (S) from race 2.3.4. The line 59-R (Cf-1, Cf-3) is susceptible to this race.

2.3.4 differs from the preceding race by the moderately resistant reaction of varieties with gene Cf-1, although the level of this resistance is higher in the variety Stirling Castle than in LMR-1. The varieties F-101 and 59-R exhibit a distinct resistance reactions. This race is very similar to the Canadian race 12 and the Dutch 2.3.4 one.

DISCUSSION

The physiological specialization of *C.fulvum* is a classical example which may in general outline be considered in the light of current

views concerning specific resistance (Flor 1960; Person 1960; Robinson 1969).

Although for the identification of the races of *C. fulvum* genes Cf-1 and Cf-3 continue to be used, however, since their practical efficiency is low and owing to the epistatic effect of stronger genes (Cf-2, Cf-4, Cf-5), they have been eliminated from breeding material, contrary to the intentions of the breeders. It appeared that the Canadian varieties on which breeding had long been based also in other centres, posses only genes controlling immunity — such as Cf-2 and Cf-4 (Patrick, Kerr and Bayley 1971). The breeding material of the fifties was usually tested with only one race (1.2.3) representing the whole group and selected only for immunity. Recently an immune gene, Cf-5 is used in breeding and several other strong genes have been identified (Kerr, Patrick, Bayley 1971; Lenhardt and Kerr 1972). Thus the further line of resistance breeding may be forseen.

Physiological specialization of the pathogen population is going on for a long time as the result of selective pressure of exclusively immune genes, and other minor differences will gradually disappear. Practically only such differences are trapped which essentially influence the currently cropped varieties. Further differentiation is only the result of tedious and fine studies. For resistance breeding in the nearest future — and it is for this purposes that races are distinguished — it seems to be quite sufficient and even necessary from practical point of view to identify a smaller number of more characteristic units by means of only the practically useful strong genes notwithstanding how they will be described. The presence or lack of the appropriate resistance gene in test variety (expressed fenotipically as resistance or susceptibility) is the basic criterion on which the races are differentiated, after all. Therefore, disregarding the practically unimportant differences, the here distinguished races could be denoted only by the main categories "4" and "2.4" (instead of the previously used 1.4 and 2.3.4 and 1.2.3.4) or only "B" and "C", according to Hubbeling (1971).

In the set of differential test varieties for the fungus races certain gene combinations are still missing, for instance Cf-1 Cf-2 Cf-3. The traditionally used veriety F-101 for which the presence of all these genes were ascribed cannot have the Cf-2 gene because it shows only moderate resistance to the races towards which Cf-2 dirrects immunity. The level of relative resistance in F-101 to the strains identified here as races 1.4 and 2.3.4 is low but distinctly lower than in 'Stirling Castle'. For the before mentioned reassons identification of some races, in spite of the clear principles, requires much experience.

It is characteristic that, with only one exception (race 11 in Canada which "changed" the immunity of the variety Vinequeen to a high level

of relative resistance), the new races at the given time were detected exclusively when an extreme change in the reaction of plants (from I to S) was recovered.

The close resemblance and repeated appearance of similar or identical races in various regions is the result of basing breeding procedures on foundations elaborated always in the same centra (Vineland). In the two main tomato resistance-breeding centres races are identified on somewhat different test sets. The similarities or differences between the new races may results, at least in some cases, from the different test sets used and inaccuracies in recognizing their genotypes.

Some races (e.g. 11) cannot be included in the system based on the gene-for-gene hypothesis, and the reaction of varieties from outside the test set (with unknown genotype) becomes the criterion for their distinction. Thus, the system of *C. fulvum* races based on the gene-for-gene hypothesis can be considered as a working scheme.

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Identyfikacja nowych ras *Cladosporium fulvum* Cooke z grup B i C na pomidorach w Polsce

Streszczenie

W kontynuowanym programie prac hodowlanych stwierdzono wystąpienie rasy (*Cladosporium fulvum* Cooke) z grupy B, przełamującej efekt genu Cf-4. Rasa ta, podobna do rasy 1.4, przełamała odporność części linii pomidorów hodowlanych, pochodzących z krzyżówek z odpornymi odmianami kanadyjskimi. W latach 1973-1975 zanotowano pojawienie się ras z grupy C, przełamujących odporność pozostałych linii hodowlanych. Nowe rasy z grupy C (jedna podobna do rasy 2.3.4., druga do hipotetycznej rasy 1.2.3.4.) przełamały odporność odmian V-548, Vagabond, Vantage, Vendor, Virase, Revermun i innych. Z odmian odpornych na te rasy należy wymienić najnowsze serie hybrydów F_1, Cura, Jet, Extase — pochodzenia holenderskiego. Ponieważ istnieją znaczne trudności w porównywaniu ras w obrębie grup B i C, występujących w różnych krajach, a „słabe" geny Cf-1 i Cf-3 nie są już od dawna używane w hodowli, autor dyskutuje możliwość pominięcia wyróżniania ras w obrębie grup.