

INHERITANCE OF RESISTANCE TO *PSEUDOPERONOSPORA CUBENSIS* ROST. IN CUCUMBER (*CUCUMIS SATIVUS* L.)

G. J. A. VAN VLIET and W. D. MEYSING

Sluis & Groot Seed Company, Enkhuizen, the Netherlands¹

Received 21 November 1973

SUMMARY

Since June 1973 *Pseudoperonospora cubensis* (BERK & CURT) ROST., which causes downy mildew in cucumber, occurs in the Netherlands. The resistance against this disease appears to be based on one recessive gene in linkage with the dominant gene *D* for dull green fruit skin colour. It is demonstrated that this recessive gene is also linked with one of the genes for resistance to powdery mildew present in the variety Ashley.

The powdery mildew resistant lines tested are also resistant against downy mildew, the linkage with the gene *D* having been broken.

INTRODUCTION

Downy mildew of cucumber, caused by *P. cubensis* (BERK & CURT) ROST., is an important disease in the eastern United States, southern Europe and, since June 1973, in the Netherlands. It spreads by means of the wind and the cucumber beetle, the latter of which does not occur in the Netherlands.

COCHRAN (1937), using the variety Bangalore as a source of resistance, assumed that the resistance was conditioned by several factors. JENKINS (1942, 1946) made crosses with the resistant varieties Chinese Long and Puerto Rico 37 and established that the resistance was of polygenic origin. Another source of resistance is PI 197087 of which the resistance according to BARNES & EPPS (1954), is polygenic. According to SHIMIZU (1962, 1963) the resistance of Aojihai is inherited as a triple recessive and appears to be linked with a dull green fruit skin colour. SITTERLY (1972) classes the varieties Poinsett and Ashley as highly resistant and resistant respectively.

The inheritance of the resistance still constitutes a problem. A better understanding of its nature will facilitate the breeding of resistant varieties with a Dutch type of fruit. For this reason the present study was undertaken.

MATERIAL AND METHOD

The resistant parent in the experiment was the variety Poinsett, line 4285 serving as susceptible partner. The former is resistant to powdery mildew as well as to downy mildew and has a dull green fruit skin colour. Line 4285 is susceptible to both diseases and its fruit skin colour is a shining green.

To investigate the inheritance of *P. cubensis* we made an F_1 , BC_1 populations with

¹ Stationed at Breeding Station Pannevis B.V., De Lier, the Netherlands.

the susceptible and the resistant parent, an F_2 , F_2BC_1 lines and F_3BC_1 lines. Line 4285 PMR is an F_6 , resistant against powdery mildew, *Sphaerotheca fuliginea* (SCHLECHT. ex FR.) POLL., and with shining fruit skin colour. It was used in crosses with the varieties Poinsett and Ashley, which are resistant against both powdery mildew and downy mildew, in order to obtain F_1 's.

In addition, a number of powdery mildew resistant inbred lines and several varieties of foreign origin were tested.

Fifteen-day old seedlings, grown in 12 cm plastic pots of a standard potting-soil, were inoculated in the afternoon. The spore-suspension for the experiment was prepared immediately before inoculation. A cucumber-leaf, well-covered with spores, was immersed in a small dish of water and the sporangia were removed by rubbing with the fingers. The suspension was passed through cheese-cloth and hand-sprayed over the cotyledons and over the under-surface of the first leaf of the plants to be tested, until run off. Once the plants had been inoculated, they were put in a polythene tent during the night and the ensuing day at a relative humidity of about 100%. The morning thereafter the tent was opened and remained so for the rest of the day. Late in the afternoon the plants were moistened with a hand-spray followed by the closing of the tent. This procedure was repeated till the cotyledons of the susceptible test plants had withered and the amount of spores gave the first leaf a black appearance. Three to four days after inoculation the cotyledons and first leaf clearly showed yellow spots.

The plants were classed very susceptible ($++$), moderately susceptible ($+$) or resistant ($-$). The criterion for resistance was that there were no spores or hardly any (BARNES & EPPS, 1950).

RESULTS

Table 1 gives the results for Poinsett, line 4285 and their progenies. Poinsett was fairly resistant. The cotyledons remained green, with small necrotic spots, while the first leaf bore yellow specks on which very little or no sporulation could be observed. With line 4285 the cotyledons grew completely yellow. Subsequently they became covered with spores, turned brown quickly and shriveled. On the first leaf big yellow areas appeared, which, at a later stage, fused and became completely covered with spores. The F_1 reacted in a way almost similar to that of the susceptible parent. However, the withering of cotyledons and the fusion of yellow areas proceeded less rapidly (see Fig. 1 and BARNES, 1961). Of the BC_1 with the susceptible parent half the number of plants was as susceptible as the susceptible parent, while the other half showed the F_1 phenotype. The BC_1 with the resistant parent segregated in a 1:1 ratio, wherein half the population corresponded with the F_1 in phenotype and the remainder of the plants was almost as resistant as Poinsett. The F_2 was found to segregate into 3 (susceptible and moderately susceptible): 1 (resistant). The moderately susceptible plants were hard to distinguish from the susceptible ones and are therefore represented by one figure in Table 1.

Three of the 6 F_2BC_1 lines did not segregate at all and were wholly susceptible. The remaining three, 4400, 4402 and 4404 segregated in 3:1. The 3 F_3BC_1 lines are the progeny of resistant F_2BC_1 plants. Two of these, 4834 and 4835, were wholly resistant,

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Table 1. Segregation for resistance to *Pseudoperonospora cubensis* in F2 and backcross populations derived from crosses of resistant (Poinsett) and susceptible (4285) cucumbers.

No	Progeny or variety	Number of plants tested	Number of plants*:			Calculated			χ^{2**}	
			++	+	-	rate	++	+		-
4359	Poinsett = P	20			20					
4382	'4285'	20	20							
4362	F1 (P × 4285)	40	40							
4364	BC1 (P × 4285) × 4285	90	48	42	1:1	45	45		0.40	
4829	BC1 (P × 4285) × P	30		16	1:1		15	15	0.13	
4363	F2 (P × 4285)	210	155	55	3:1	157.5		52.5	0.52	
4399	F2BC1 (P × 4285) × 4285	65	65							
4400	F2BC1 (P × 4285) × 4285	67	57	10	3:1	50.3		16.8	3.64	
4401	F2BC1 (P × 4285) × 4285	65	65							
4402	F2BC1 (P × 4285) × 4285	56	40	16	3:1	42		14	0.38	
4403	F2BC1 (P × 4285) × 4285	65	65							
4404	F2BC1 (P × 4285) × 4285	56	43	13	3:1	42		14	0.095	
4834	F3BC1 (P × 4285) × 4285	40		40						
4835	F3BC1 (P × 4285) × 4285	40		40						
4836	F3BC1 (P × 4285) × 4285	40	9	22	8	1:2:1	10	20	10	0.7

*++ = very susceptible; + = moderately susceptible; - = resistant.

** χ^2 (1:1) (3:1) < 3.84, P = 0.05; χ^2 (1:2:1) < 5.99, P = 0.05.



Fig. 1. Susceptibility or resistance to *Pseudoperonospora cubensis*. 4392, Bitspot, susceptible; 4393, Poinsett, resistant; 4394, F₁ (Poinsett × Bitspot) moderately susceptible.

while the third, 4836, obviously derived from a wrongly judged F_2BC_1 plant, segregated in 1:2:1. The moderately susceptible individuals in this progeny could be distinguished from the susceptible ones.

The ratios of segregation show that the resistance is conditioned by one recessive gene.

Of the resistant F_2 plants 30 were set out in the greenhouse. It appeared that the 30 plants were fairly resistant against powdery mildew and, in addition, bore dull green fruit. An F_2 population which had not been tested for resistance to both mildews segregated into a quarter for shining fruit skin colour (KOOISTRA, 1971; own experience). The F_2BC_1 's 4399, 4401 and 4403, which were wholly susceptible, derived from BC_1 plants with shining fruit skin colour, while the segregating lines 4400, 4402 and 4404 arose from BC_1 plants with dull green fruit skin colour. Of the BC_1 population with the susceptible parent three moderately susceptible and three susceptible individuals were planted in the greenhouse. The former three had a higher level of resistance against powdery mildew than the latter. Therefore the gene for downy mildew resistance is linked to the gene D of KOOISTRA (1971). KOOISTRA found that one of the genes for resistance to powdery mildew was linked to the gene D. From Table 2 it appears that Poinsett and Ashley both are resistant against downy mildew. In Poinsett however the level of resistance was higher than in Ashley, which can be seen from their F_1 's in crosses with 4285. The F_1 from Ashley \times 4285 is more susceptible than the F_1 from Poinsett \times 4285. The F_1 population resulting from Poinsett

Table 2. Susceptibility or resistance to *Pseudoperonospora cubensis* of some varieties and the F_1 's of Poinsett and Ashley with powdery mildew resistant line 4285 (4285 PMR).

No	Progeny or variety	Number of plants tested	Number of plants*:		
			++	+	-
4826	Poinsett	20			20
4832	'4285'	20	20		
4831	F_1 (Poinsett \times 4285 PMR)	30			30
4360	Ashley	20			20
4395	F_1 (Ashley \times 4285)	20	20		
4373	F_3BC_1 (BV \times PMR) \times BV	30			30
4374	F_2 (B \times PMR)	30			30
4375	F_3 (B \times PMR)	30			30
4376	F_2 (B \times PMR)	30			30
4377	F_8 (Sp \times PMR)	30			30
4378	F_3 (Sp \times PMR)	30			30
4379	F_3 (Sp \times PMR)	30			30
4383	F_4 (Best \times PMR)	30			30
4384	F_4 (Best \times PMR)	30			30
4361	Chipper	20			20
4367	Natsufushinari	20			20
4389	M72/119 from Japan	20			20
4390	M72/116 from Japan	20			20
4385	Soryu	20			20
4386	Langelands Giant	20	20		
4388	Butchers Disease Resister	20	20		

* ++ = very susceptible; + = moderately susceptible; - = resistant.

× 4285 PMR is resistant against downy mildew. Our PMR inbred lines appear also to be downy mildew resistant, although the linkage with dull green fruit skin colour has been broken.

The above data show that one of the genes for resistance against powdery mildew is linked with the recessive gene conditioning downy mildew resistance.

According to SITTERLY (1972) the variety Ashley possesses one gene for PMR, which therefore must be the gene in question. This gene has been found in Poinsett, Ashley and our PMR lines.

DISCUSSION

What is known so far about the inheritance of resistance against *P. cubensis* is mainly based on field tests, which do not always allow a clear distinction of very susceptible, moderately susceptible and resistant. BARNES & EPPS (1950) observed that the degree of sporulation in resistant varieties largely depends on the age of the plant and on the concentration of the inoculum. COHEN & ROTEM (1971a, 1971b) demonstrated that low temperature, high light-intensity and extended day-length enhance the sporulating potential, the formation of sporangia requiring a period of darkness and moisture.

The greenhouse seedling test applied in this investigation minimized the environmental variability and as a result the inheritance of resistance could probably be revealed more accurately. The resistance investigated here is not a type of immunity since limited growth and sporulation of the fungus was observed on resistant plants.

It is proposed to designate the gene for resistance to downy mildew as *p* and the gene for resistance to powdery mildew, which is linked to the former, as *s*.

It could well be that the genes *p* and *s* are identical, in which case we are dealing with pleiotropy. Further research will have to prove such.

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