Inheritance of Resistance to Powdery Mildew in Cucumber

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ABSTRACT

Resistance to powdery mildew in cucumber is controlled by a major recessive gene *s*. This recessive gene *s* determines hypocotyl (intermediate) resistance and is also essential for leaf (complete) resistance. Leaf resistance is controlled by dominant gene *R*, which only expresses itself in the presence of recessive gene *s*. Gene *I* is an inhibitory gene which prevents the expression of complete resistance, but does not affect gene *s*. The genes responsible for resistance in cultivars P.I. 212233, P.I. 234517, and Natsufushinari appear to be the same. Genes for powdery mildew resistance, scab resistance, cotyledon bitterness, and spine color are all independently inherited, and no linkage was observed between them. Phytopathology 61:1218-1221.

Additional key words: Cucumis sativus, gene linkages.

Powdery mildew is an important disease both on field and greenhouse-grown cucumbers (12). Both *Erysiphe cichoracearum* DC. ex Merat emend. Salm. and *Sphaerotheca fuliginea* (Schlecht. ex Fr.) Poll., have been implicated as causal agents of powdery mildew (3, 4, 5, 6, 7, 8). In the absence of the sexual stage, it is difficult to distinguish between these two fungi.

Resistance to powdery mildew has been reported in a number of cucumber accessions from Asia (4, 5, 7, 13, 14). Based on an F_2 population of about 100 plants, Smith (10) proposed that the resistance of the cultivar Puerto Rico 37 was probably polygenic. Barnes & Epps (4), in developing resistant cucumber cultivars, suggested that resistance in P.I. 197087 was due to one or two major genes and one or two minor genes (3). A single recessive gene was shown to be responsible for the resistance in the Japanese cultivar Natsufushinari (5). Resistance of the cultivar Yomaki from Japan was attributed to two pairs of duplicate recessive genes (14). After observing highly resistant segregates from a cross of two parents with only intermediate resistance, Kooistra (7) proposed that three recessive genes controlled this high resistance. Two genes came from Natsufushinari and one from P.I. 200815. In our cucumber breeding program, there were lines which could be consistently classified as highly resistant, intermediate, and susceptible. These were used to study the inheritance of resistance to the biotypes of powdery mildew found in Wisconsin.

A study of linkage relationships among powdery mildew resistance, scab resistance, fruit spine color, and cotyledon bitterness were included.

Materials and Methods.—Cucumber, *Cucumis sativus* L., seedlings in the cotyledonary leaf stage were inoculated in the greenhouse by dusting with conidia of powdery mildew from heavily mildewed leaves on 3 consecutive days. Inoculum throughout this study was derived from a single conidial culture of *S. fuliginea* isolated from greenhouse-grown cucumbers in Wisconsin, and maintained in the greenhouse by serial inoculations of susceptible plants. In all the tests, either Chicago Pickling or Straight Eight was included as a susceptible control. Three to 4 days after the first inoculation, growth of powdery mildew became visible on the cotyledons of control plants. Seven to 12 days after inoculation, the cotyledons and hypocotyl of susceptible plants were heavily infected. On the plants classified as susceptible, the cotyledons, hypocotyl, upper and lower side of the true leaves, stem, and petiole were completely covered with powdery mildew. The cotyledons and true leaves on plants classified as intermediate were infected either mildly or severely, but there was no mildew on the hypocotyl, stem, or petiole. Resistant plants either had no powdery mildew or, at most, one or two weak colonies which elicited a hypersensitive necrosis in the leaf tissue beneath.

Twenty accessions of cucumber, previously reported resistant to powdery mildew, were screened in the greenhouse. From these, six were selected for genetic and linkage studies based on their reaction to powdery mildew and various other phenotypic characters (Table 1). Crosses were made between all combinations of the six lines (Table 2). Crosses, selfs of the F_1's, and backcrosses were made in the greenhouse. During the summer, seed of the parent, F_1, F_2, and BC_1 populations were germinated in 2.5-inch peat pots in the greenhouse. Seedling plants were inoculated with powdery mildew, and 10-15 days later transplanted to the field.

Three readings were made to insure that plant reactions did not change as the result of different biotypes in the field. An initial reading for powdery mildew severity was taken before transplanting to the field, and a second reading was taken in the field 3 weeks after transplanting. A final powdery mildew rating was made when the data on spine color of mature fruit were collected.

In crosses where nonbitter and bitter cotyledon segregation was expected, the seeds were germinated in

TABLE 1. Phenotypes of cucumber plants selected for studies on powdery mildew resistance and linkage relations among powdery mildew resistance, scab resistance, fruit spine color, and cotyledon bitterness

Parents	Source	Cotyledon bitterness	Powdery mildew reaction	Scab reaction	Fruit spine color
Line 9362 (P_A)	Wisconsin	Nonbitter	Resistant	Resistant	Black
P.I. 212233 (P_B)	Japan	Bitter	Intermediate	Resistant	White
P.I. 234517(P_C)	South Carolina	Bitter	Resistant	Susceptible	White
Chicago Pickling (P_D)		Bitter	Susceptible	Susceptible	Black
Pixie (P_E)	South Carolina	Bitter	Intermediate	Susceptible	White
Natsufushinari (P_F)	Japan	Bitter	Resistant	Susceptible	White

vermiculite. We classified the plants as bitter or nonbitter by tasting the cotyledons, then transplanted them to 2.5-inch peat pots. Fruit spine color data were collected from the field. If plants were to be screened for resistance to scab, *Cladosporium cucumerinum* Ell. & Arth., seeds were germinated in 2.75-inch peat pots in the greenhouse. Plants were classified as bitter or nonbitter, then inoculated with powdery mildew. After 15-20 days under a 16-hr photoperiod at 26-30 C, the seedlings were classified for mildew resistance, then inoculated with *C. cucumerinum* as described by Walker (11). Four to 5 days after inoculation, readings for scab resistance were recorded.

RESULTS.—Although the perfect stage was not observed either in the greenhouse or the field, our observations on various morphological characteristics of the asexual stage agree with those described by Kable & Ballantine (6), suggesting the fungus is *S. fuliginea*. Reactions of various genotypes studied did not vary between the first reading in the greenhouse and the final field reading, suggesting that a single biotype of the fungus was being studied.

Of the 20 accessions reported to have various levels of powdery mildew resistance, 10 had at least some plants which were classified as resistant or intermediate.

The individual plants of each of the six parents selected for the genetic study, when selfed, bred true for each of the characters for which it was chosen (Table 1).

The F_1, F_2, and BC progenies from crosses between resistant 9362 (P_A) $\times$ resistant P.I. 234517 (P_C), resistant $P_A \times$ resistant Natsufushinari (P_F), and $P_C \times P_F$ were all resistant, suggesting that genes governing resistance were the same in all three lines. The cross between the intermediate type P.I. 212233 (P_B) and intermediate Pixie (P_E) produced only intermediate resistance. The F_1 from crosses between resistant 9362 (P_A) and intermediate P.I. 212233 (P_B), or resistant P_A and intermediate Pixie (P_E), were all intermediate for resistance; and F_2 population segregated as 13 intermediate and 3 resistant (Table 2). The F_1 between resistant $P_A \times$ intermediate P_B, or resistant $P_A \times$ intermediate P_E, when backcrossed to resistant P_A, segregated resistant to intermediate as 1:1. However, crosses $P_A \times P_B$ or $P_A \times P_E$ backcrossed to intermediates P_B and P_E, respectively, gave all intermediate plants.

In the cross between resistant 9362 (P_A) and susceptible Chicago Pickling (P_D), all F_1 plants were susceptible. The F_2 population segregated as 12 susceptible, 3 intermediate, and 1 resistant. The cross between $P_A \times P_D$ backcrossed to resistant P_A segregated 2 susceptible, 1 intermediate, and 1 resistant; whereas the backcross to susceptible P_D produced all susceptible plants.

The segregation patterns for scab resistance, fruit spine color, and cotyledon bitterness conformed closely with that reported in the literature (1, 2, 5, 9, 11) for each character (Table 2), and no linkage was found between any characters examined (Table 3).

DISCUSSION.—Based on the segregation ratios observed in this study, the most logical explanation of resistance appears to be that the principle gene *s* is recessive. This recessive *s* gene determines hypocotyl (intermediate) resistance and is also essential for leaf (complete) resistance. Leaf (complete) resistance is controlled by dominant gene *R*, which only expresses itself in the presence of recessive gene *s*. Gene *I* is an inhibitor gene which prevents the expression of complete resistance, but does not affect gene *s*. Therefore, the resistant lines 9362, P.I. 234517, and Natsufushinari have the genotype *RR ii ss*. Segregation data suggests that the genotype of susceptible Chicago Pickling is *RR II SS*, whereas that of intermediate resistant P.I. 212233 and Pixie is *rr II ss*.

The relative clarity with which three distinct classes of resistance could be identified in our material provided a firm basis for postulating the inheritance of resistance to the biotype of powdery mildew found in Wisconsin.

The inheritance patterns postulated in this work show remarkable similarities between those reported in the literature, and may perhaps provide a basis for comparison of resistant genotypes examined by others. Though Smith (10) reported resistance to be polygenic, with only 100 plants in an F_2 population he may have been unaware of the three classes reported herein. Barnes & Epps (4), in reporting one or two major genes and one or two minor genes, may have been considering *R* or *S* as a major gene and the others with *I* as the two minor genes. The single recessive gene for resistance reported by Hujieda & Akiya (5) could have been *s* in which the two parents were homozygous for *R* and *I*. Warid et al. (13), in reporting

TABLE 2. Inheritance of resistance to *Sphaerotheca fuliginea*, *Cladosporium cucumerinum*, cotyledon bitterness, and fruit spine color in cucumber

	Cotyledon bitterness[a]		Expected ratio			Powdery mildew[b]			Expected ratio			Scab[b]		Expected ratio			Fruit spine color		Expected ratio		
Parents	B	NB	B:NB	X^2	*P*	R	I	S	R:I:S	X^2	*P*	R.	S.	R:S	X^2	*P*	Bl	W	Bl:W	X^2	*P*
9362 (P_A) × P.I. 212233 (P_B)	50	0				0	50	0									50				
P_A × P.I. 234517 (P_C)	20	0				20	0	0									20				
P_A × Chicago Pickling (P_D)	20	0				0	0	20									20				
P_A × Pixie (P_E)	25	0				0	25	0				25					25				
P_A × Natsufushinari (P_F)	20	0				20	0	0									20				
$P_B \times P_E$						0	20	0													
($P_A \times P_B$) selfed	300	108	3:1	.460	.50	69	339	0	3:13	.89	.35						386	22	15:1	.52	.50
($P_A \times P_D$) selfed	153	45	3:1	.530	.40	7	36	155	1:3:12	2.64	.30						198	0			
($P_A \times P_E$) selfed	230	81	3:1	.181	.70	55	256	0	3:13	.024	.85	240	71	3:1	.078	.80					
($P_A \times P_B$) × P_A	37	34	1:1	.124	.75	32	39	0	1:1	.68	.40						71	0			
($P_A \times P_B$) × P_B	93	0				0	93	0									70	23	3:1	.001	.95
($P_A \times P_D$) × P_A	30	27	1:1	.140	.70	9	16	32	1:1:2	2.57	.30						57	0			
($P_A \times P_D$) × P_D	52	0				0	0	52									52	0			
($P_A \times P_E$) × P_A	26	28	1:1	.062	.85	21	33	0	1:1	2.66	.15						54	0			
($P_A \times P_E$) × P_E	83	0				0	83	0									41	42	1:1	.012	.90

[a] Bitter = B; nonbitter = NB; fruit spine color: Bl = black; W = white.
[b] R = Resistant; I = intermediate; S = susceptible.

TABLE 3. Analysis of linkage relationships among powdery mildew (PM) resistance, scab resistance, cotyledon bitterness, and fruit spine color in cucumber

Parents[a]	PM-intermediate		PM-resistant		Expected ratio	X^2	P
	Bitter	Non-bitter	Bitter	Non-bitter			
F_1 ($P_A \times P_B$) selfed	251	88	49	20	39:13:9:3	1.59	.60
F_1 ($P_A \times P_E$) selfed	189	60	41	21	39:13:9:3	3.16	.40
($P_A \times P_B$) $\times P_A$	17	22	20	12	1:1:1:1	3.16	.40
($P_A \times P_E$) $\times P_A$	15	18	11	10	1:1:1:1	3.02	.40

Parents	Black spine		White spine		Expected ratio	X^2	P
	PM-intermediate	PM-resistant	PM-intermediate	PM-resistant			
F_1 ($P_A \times P_B$) selfed	318	68	21	1	195:45:13:3	3.29	.40

Parents	Black spine		White spine		Expected ratio	X^2	P
	Bitter	Non-bitter	Bitter	Non-bitter			
F_1 ($P_A \times P_E$) selfed	285	101	15	7	45:15:3:1	1.26	.75

Parents	Bitter		Nonbitter		Expected ratio	X^2	P
	Scab-resistant	Scab-susceptible	Scab-resistant	Scab-susceptible			
F_1 ($P_A \times P_E$) selfed	176	54	64	17	9:3:3:1	1.19	.80

Parents	PM-intermediate		PM-resistant		Expected ratio	X^2	P
	Scab-resistant	Scab-susceptible	Scab-resistant	Scab-susceptible			
F_1 ($P_A \times P_E$) selfed	192	64	48	7	39:13:9:3	4.36	.25

Parents	PM-susceptible		PM-intermediate		PM-resistant		Expected ratio	X^2	P
	Bitter	Non-bitter	Bitter	Non-bitter	Bitter	Non-bitter			
F_1 ($P_A \times P_D$) selfed	117	38	30	6	6	1	36:12:9:3:3:1	4.15	.50
($P_A \times P_D$) $\times P_A$	19	13	6	10	5	4	2:2:1:1:1:1	5.00	.45

[a] P_A = 9362; P_B = P.I. 212233; P_C = 234517; P_D = Chicago Pickling; P_E = Pixie; P_F = Natsufushinari.

duplicate recessive genes, may have been examining the *s* gene and a fourth gene which could have been homozygous recessive in all our lines, while *R* and *i* could have been homozygous dominant and recessive, respectively, in both parents. The three recessive genes reported by Kooistra (7) could have been *i* and *s* genes in this study together with the other gene indicated by Warid et al. Thus, by the addition of one recessive gene to the gene system proposed here, the apparently divergent inheritance patterns described in the literature could be unified.

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