Factors Affecting Penetrance of Resistance to Fusarium oxysporum f. sp. lycopersici in Tomatoes

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ABSTRACT

Resistance of tomatoes to *Fusarium oxysporum* f. sp. *lycopersici* is based on the action of a single dominant gene (*I*). Penetrance of resistance is incomplete, however, since various proportions of diseased seedlings are found in resistant lines. Penetrance is affected by the interaction between host genotype and inoculum concn, seedling age, or soil temp. As a general trend, an increase in inoculum concn causes a decrease in penetrance, i.e., an increase in disease incidence, but the susceptible cultivar 'Marmande' (*ii*) was affected at much lower concns than the homozygous (*II*) 'Roma VF' or 'Homestead 24'. The heterozygous (*Ii*) hybrids showed a lower penetrance than their respective homozygous resistant parents, and resistance in Roma VF was of lower penetrance than that in Homestead 24. Penetrance in the resistant cultivars was the lowest when seedlings were at ages of 2 or 5 days postemergence, whereas Marmande showed a complete susceptibility at all ages tested. At soil temp ranging 17-20 C, disease incidence among resistant cultivars and hybrids was higher than that at 27-30 C; the opposite was true for Marmande. Diseased seedlings of heterozygous resistant plants were less affected than diseased plants of Marmande in terms of disease progress, water conductivity in the vessels, population level, and distribution of the pathogen in various plant parts.

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Resistance of tomato cultivars to race 1 of *Fusarium oxysporum* f. sp. *lycopersici* depends on the action of a single dominant gene (*I*) derived from *Lycopersicon pimpinellifolium* (4). In some cases, however, diseased plants were found in homozygous (*II*) or heterozygous (*Ii*) plants (1, 4, 5, 12, 16, 18). Bohn and Tucker (4) suggested that incomplete dominance was involved. Retig et al. (16) found about 38% disease incidence in an F_1 population heterozygous for resistance, and attributed the results to incomplete penetrance. Penetrance (of a gene) is defined as the proportion of individuals of a given genetical constitution in a given population, in which the phenotypic effect of the gene concerned distinguishes them from those bearing its allelomorph. Thus in the case of incomplete penetrance in resistant tomato cultivars, the gene for Fusarium resistance is phenotypically expressed only in a certain percentage of the population, whereas complete penetrance denotes no disease in inoculated

plants. Penetrance was usually lower in heterozygous than in homozygous lines and was affected by environmental conditions (12, 16).

Fusarium wilt of tomatoes was affected by a variety of conditions; e.g., inoculum concentration, temp and genotype of the cultivar (21). Studies of the disease have shown that after invading the tissues, the pathogen spreads upwards throughout them, accompanied by significant changes in the plant; e.g., xylem discoloration and decrease in water conductivity (21). Most studies have been with susceptible cultivars, paying less attention to the occasional diseased plants of resistant genotypes.

This study deals with the various factors affecting the degree of penetrance of Fusarium wilt resistance in tomatoes, and characterizes the differences in disease development between plants of different resistance-genotypes.

MATERIALS AND METHODS.—*Inoculation and pathogenicity tests.*—A virulent isolate of *Fusarium oxysporum* f. sp. lycopersici (Sacc.) Snyd. & Hans. race 1, originally derived from a wilted field-grown tomato plant was grown on yeast extract dextrose agar for 8 days at 28 C. The fungal mats were then scraped from the agar, and the conidia separated from the mycelium by filtering through cheesecloth. The conida were washed twice by centrifugation. Unless otherwise stated, the inoculum concn used was 2×10^6 conidia/ml, adjusted according to hemocytometer counts. Tomato seeds, surface disinfested with sodium hypochlorite, were sown in methyl-bromide-treated soil. Eight days after sowing (2 days after emergence) the seedlings were removed from the soil, and their roots were washed in tap water. The roots of 100 seedlings of each cultivar were dipped for 1 min in the conidial suspension. They were then transplanted in four replicates to methyl-bromide-treated loamy sand soil, and grown for an additional 25 days in a greenhouse at temperatures of 25-31 C. Diseased seedlings, usually detected from 7 days after inoculation, were marked daily. From the cumulative curve obtained, the number of days required to obtain 50% of the final maximum disease incidence was calculated. Typical *Fusarium oxysporum* cultures were always obtained from plated, randomly selected, diseased seedlings from all cultivars, and pathogenicity tests reconfirmed their classification as race 1. Noninoculated seedlings of all cultivars maintained at identical conditions, remained healthy.

Tomato cultivars used were a local line of the susceptible (*ii*) Marmande, the resistant (*II*) Homestead 24 (Ferry-Morse, USA), and (*II*) Roma VF (Asgrow, USA) as well as the respective heterozygous (*Ii*) F_1 hybrids. In the hybrid seed production, the resistant cultivars served as females.

The effect of seedling age at time of inoculation on the degree of penetrance was tested by sowing the cultivars at various dates and inoculating them simultaneously. The effect of soil temp was tested by growing the inoculated seedlings in plastic pots immersed in "Wisconsin temperature tanks".

Xylem water-conductibility.—Stems of healthy and diseased plants were cut at their bases and placed in a 1% aqueous solution of eosin (17) for 20 and 45 s, respectively. They were then removed, and freehand sections were cut to determine dye distribution. Flow rate of the dye solution in the xylem was expressed as mm/min.

Rate of pathogen colonization of plant tissues.—A direct assessment of the number of the pathogen propagules per g of dry matter of the plant tissue (85 C) was made after tissue maceration and dilution on a selective medium (11). Relative rates of tissue colonization was also determined by plating 2-mm-long, surface-sterilized tissue segments on the selective medium, and calculating the percentage of *Fusarium* colonization (11).

All experiments were carried out twice or more with similar results. Statistical analysis was based on Duncan's multiple range test.

RESULTS.—*Effect of inoculum concn and resistance-genotype.*—Tomato seedlings of five cultivars were inoculated 2 days after emergence with conidial suspensions of the pathogen. Tests with various concns (Table 1) showed that both genotype and inoculum concn, had pronounced effects on

TABLE 1. Effect of inoculum concn of *Fusarium oxysporum* f. sp. *lycopersici* on percentage of diseased seedlings of five tomato cultivars and hybrids[a]

Cultivar or hybrid	Genotype	Expected reaction	Inoculum concn, conidia/ml					
			5×10^3	10^4	5×10^4	10^5	10^6	2×10^6
Marmande	*ii*	Susceptible	67	75	81	96	95	97
Homestead 24	*II*	Resistant	0	0	0	0	0	2
Homestead 24 × Marmande	*Ii*	Resistant	2	4	5	8	19	43
Roma VF	*II*	Resistant	4	8	14	16	19	31
Roma VF × Marmande	*Ii*	Resistant	20	26	32	41	50	63

[a]At each inoculum concn tested, 100 seedlings of each cultivar or hybrid were inoculated.

disease incidence, and hence, on the penetrance of the resistance gene. Though the three cultivar and two hybrid populations responded differently, an increase in inoculum concn usually caused a decrease in penetrance; i.e., an increase in disease incidence. At spore concn of 10^5/ml, 96% of the seedlings of the susceptible Marmande were rated susceptible, while the two homozygous resistant cultivars Homestead 24 and Roma VF gave rates of 0 and 16%, respectively. The resistant cultivar Roma VF and the two F_1 populations showed a decreased penetrance of resistance upon increasing inoculum concn, but at levels much higher than those effective for Marmande. The resistance genotype affected the degree of penetrance as follows: heterozygous populations showed lower penetrance than their respective homozygous resistant parents, and resistance in Roma VF was of lower penetrance than that in Homestead 24. Similarly, the heterozygous F_1 with Roma VF was more susceptible than the corresponding hybrid with Homestead 24.

The increase in disease incidence after inoculation was more rapid in the susceptible cultivar than in those with one or two alleles for resistance (Fig. 1); e.g., 50% of maximum disease incidence in Marmande (*ii*) and cultivars with *I* genes, was reached 10 and 15-19 days after inoculation, respectively.

The relatively high susceptibility of Roma VF and its F_1 cross, suggested the possibility of seed contamination or of lack of homozygosity of their gene *I*. It can be seen, however, that in these lines, unlike Marmande, an increase in the inoculum concn above 10^5 conidia/ml resulted in a subsequent increase in the percentage of diseased plants (Table 1). Thus, the seedlings of Roma VF and its F_1 hybrids which became diseased only at a high inoculum concn, seem to differ from Marmande. As the seeds of F_1 lines were obtained from plants in which the resistant cultivar served as female, occasional self-fertilization (if any) could only result in a surplus of homozygous resistant, but not susceptible, plants. The purity of Roma VF was tested in an additional experiment. Seedlings were inoculated with a suspension 10^6/ml spores; and, when disease symptoms were obvious, diseased and healthy seedlings were removed, washed free of soil, and replanted in individual pots filled with noninfested soil. Most of the diseased seedlings, cured by dipping the roots in 0.1% benomyl for 60 min, recovered and produced fruit. Seeds of five originally healthy, and five originally diseased plants were separately collected, sown, and served for testing the resistance to *Fusarium* compared with Marmande and Roma VF. The results (Table 2) show that disease susceptibility of all Roma VF plants from any source was 4-30% and was significantly different (at the 5% level) from Marmande which reached a susceptibility of 99%.

Effect of seedling age and resistance-genotype.—Seedlings were inoculated 2-20 days after emergence. Their age affected neither the degree of susceptibility of Marmande nor that of resistance of Homestead 24 (Fig. 2). With Roma VF and the heterozygous hybrids, however, penetrance of resistance was lowest for plants inoculated at 2 and 5 days after emergence and then increased with age.

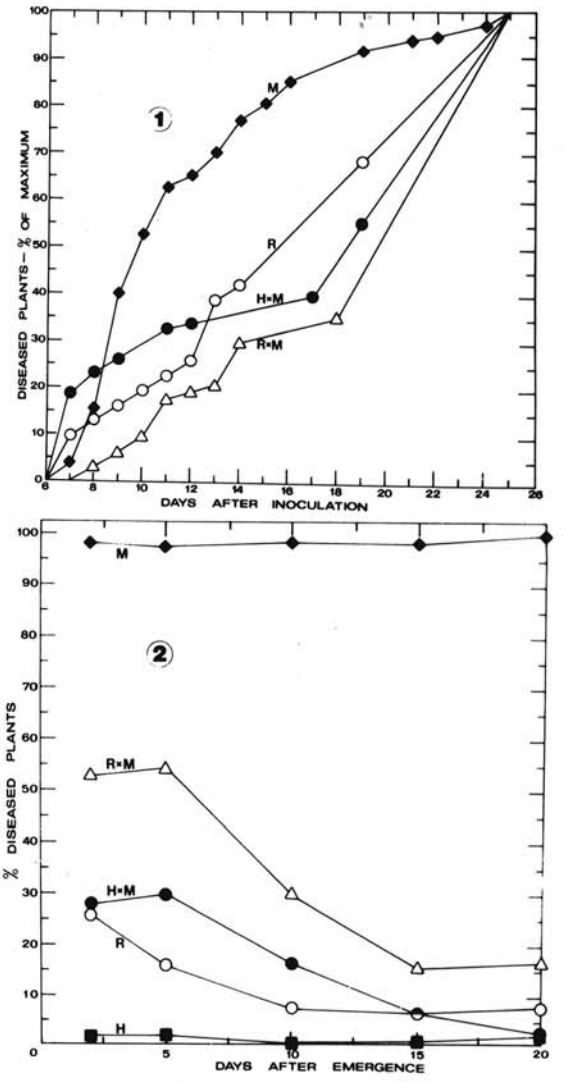

Fig. 1-2. 1) Progress of disease incidence in tomato seedlings inoculated with *Fusarium oxysporum* f. sp. *lycopersici* (2 × 10^6 conidia/ml). Cumulative curve, in percentage of the final maximum disease incidence obtained with each cultivar and hybrid. **2)** Effect of tomato seedling age (day after emergence) at time of inoculation by *Fusarium oxysporum* f. sp. *lycopersici* on disease incidence. Legend for cultivars and hybrids: Marmande (M); Roma VF (R); Homestead 24 (H); Homestead 24 × Marmande (H × M); and Roma VF × Marmande (R × M).

Effect of soil temp and resistance-genotype.—This environmental factor had pronounced and opposite effects on the percentage of diseased plants of susceptible and resistant lines (Table 3). A marked decrease in penetrance at low temp, especially at 17 C, was noted in all *I* homozygous or heterozygous lines. This contradicts the reported disease incidence reduction found in susceptible varieties at low temp

(6, 19, 21). Such a reduction, though lower, was found in the susceptible Marmande at 17 C, but it is possible that the high inoculum concn (2×10^6 conidia/ml) may have partially compensated for the effect of the low temp in that cultivar. This was shown in a separate experiment in which Marmande seedlings, inoculated at two inoculum concns, and maintained at three temp: 15, 17 and 27 C, yielded 26, 57, and 89% diseased seedlings, respectively, at inoculum concentration of 10^5 conidia/ml; and 82, 83, and 96% diseased seedlings, respectively, at inoculum concentration of 2×10^6 conidia/ml.

TABLE 2. The relative Fusarium wilt susceptibility of tomato lines derived from healthy and diseased plants. Seedlings were inoculated with inoculum suspension at a concn of 5×10^5 conidia/ml

Cultivar (genotype)	Origin	Diseased plants (%)[x]
Marmande (*ii*)	Original[y]	99 a
Roma VF (*II*)	Original	10 cd
Roma VF (*II*)	Healthy[z]	11 cd
Roma VF (*II*)	Healthy	17 bc
Roma VF (*II*)	Healthy	19 bc
Roma VF (*II*)	Healthy	19 bc
Roma VF (*II*)	Healthy	28 bc
Roma VF (*II*)	Diseased[z]	4 d
Roma VF (*II*)	Diseased	19 bc
Roma VF (*II*)	Diseased	22 bc
Roma VF (*II*)	Diseased	26 bc
Roma VF (*II*)	Diseased	30 b

[x]Numbers followed by the same letter are not significantly different, $P = 0.05$.

[y]Original seeds used throughout the experiments.

[z]Seedlings of Roma VF were inoculated with *F. oxysporum* f. sp. *lycopersici*. When symptoms were obvious, diseased and healthy plants were grown separately, seeds were recovered from each individual plant and served for testing resistance to Fusarium wilt.

Nature of the disease in plants of different genotypes.—The previous experiments show that diseased seedlings are detected, to various degrees, in susceptible as well as resistant cultivars. Thus, the response to pathogen invasion and rate of tissue colonization in diseased plants of two genotypes, *ii* and *Ii* was compared.

Water conductivity of diseased plants was more severely affected (in all three growth stages tested) in Marmande than in F_1 plants (Table 4). This is in accordance with the slower disease progress found in F_1 plants (Fig. 1). Diseased plants of resistant genotypes had fewer discolored xylem bundles than

TABLE 4. Water movement in healthy and Fusarium wilt-infected tomato seedlings of homozygous- and heterozygous-susceptible genotypes (eosin movement technique)

Cultivar or hybrid	Genotype	Plant condition	Rate of flow, mm/min[z] Days after inoculation 7	8	13
Marmande	*ii*	Healthy	113.4 a	131.4 a	128.3 a
Homestead 24 × Marmande	*Ii*	Healthy	123.0 a	135.6 a	133.2 a
Marmande	*ii*	Diseased	16.8 c	21.3 c	15.2 c
Homestead 24 × Marmande	*Ii*	Diseased	33.7 b	35.9 b	27.6 b

[z]Numbers in each colum followed by the same letter are not significantly different, $P = 0.05$.

TABLE 3. Effect of soil temperature on percentage of diseased seedlings of five tomato cultivars and hybrids inoculated with 2.0×10^6 conidia/ml of *Fusarium oxysporum* f. sp. *lycopersici*

Cultivar or hybrid	Genotype	Soil temperature, C[z] 17	20	25	27	30	34
Marmande	*ii*	88.9 [z]	96.8 a	100.0 a	100.0 a	98.4 a	18.6 b
Homestead 24	*II*	11.1 a	6.3 a	6.3 a	0.0 a	1.6 a	0.0 a
Homestead 24 × Marmande	*Ii*	38.1 a	36.5 a	25.4 a	6.3 b	4.8 b	0.0 b
Roma VF	*II*	25.4 a	22.2 a	14.3 ab	9.5 ab	4.8 b	0.0 b
Roma VF × Marmande	*Ii*	73.0 a	57.1 b	42.9 c	27.0 d	15.9 d	3.4 e

[z]For each cultivar or hybrid, figures followed by the same letter are not significantly different, $P = 0.05$.

TABLE 5. Population level of *Fusarium oxysporum* f. sp. *lycopersici* in tissues of diseased tomato seedlings of two resistant genotypes, as estimated by the dilution and the segmentation techniques

Cultivar or hybrid (Genotype)	Part of Plant[b]	A-Dilution techniques[a], 1,000 propagules/g dry tissue: Experiment no. 1	2	3	Avg	Root / Stem 2
Marmande	Root	2,391	1,818	1,051	1,753[c]	
(*ii*)	Stem 1	920	8,811	3,564	4,432[c]	1.76
	Stem 2	884	1,050	1,049	994[c]	
Homestead 24	Root	1,143	1,204	800	1,049	
× Marmande	Stem 1	316	187	485	329	14.57
(*Ii*)	Stem 2	39	135	41	72	

		B. Segment technique[d], % Fusarium infected segments: Experiment no. 1	2	3	4	Avg	Root / Stem 2
Marmande	Root	100	100	100	96	99	
(*ii*)	Stem 1	100	100	97	100	99	1.10
	Stem 2	96	96	76	93	90[c]	
Homestead 24	Root	100	100	97	100	99	
× Marmande	Stem 1	100	97	50	94	85	2.25
(*Ii*)	Stem 2	70	42	0	64	44	

[a]Tissues were macerated in a Waring Blendor, diluted, and spread over solidified agar medium. *Fusarium* colonies obtained were counted, and population density (no. propagules/g dry tissue) was calculated.
[b]Plants were cut into three sections: roots, 0-1 cm aboveground (stem 1), and 4-5 cm aboveground (stem 2).
[c]Significantly different ($P = 0.05$) from respective plant part of Homestead 24 × Marmande tested with the same technique.
[d]Plant segments (2-mm long) were plated out on agar medium and % of segments yielding *Fusarium* was determined.

the susceptible ones, and a high proportion of upward-curving cotyledons, an unusual disease symptom which was reported earlier (16).

Pathogen colonization in tissues of the diseased plants was estimated quantitatively by maceration and subsequent dilution. The results show that tissues of diseased plants of the resistant genotype were significantly less colonized by the pathogen than those of the susceptible one (Table 5). This difference between the genotypes was greatest in the upper parts of the plants; e.g., the pathogen population ratio between root and upper part of the stem was 1.76 in Marmande and 14.57 in the heterozygous F_1. Hence, the spread of the pathogen in host tissues is much more limited in diseased plants of the resistant genotype. Results obtained by the segmentation technique (Table 5) show that only in the upper stem parts, was colonization by the pathogen significantly higher in Marmande than that in the heterozygous resistant line. This technique, however, does not express the degree of colonization of individual plant parts.

It is well established that the pathogen may invade the tissues of resistant plants with no disease symptoms (2, 11, 15). The rate of colonization of apparently healthy inoculated plants of homozygous and heterozygous resistant genotypes was compared. The results show that pathogen-colonization in tissues of these healthy plants was, as expected, much less intensive than that of tissues of diseased plants, and that the pathogen was restricted mainly to the roots (Table 6). No significant difference was observed between the resistant cultivars, but there was an indication that in the homozygous resistant type the lower part of the stem (stem 1) is less colonized than in the heterozygous one.

DISCUSSION.—In this work, the degree of penetrance in tomato cultivars possessing one or two alleles for Fusarium resistance, varied between 100% and 27% in an extreme case (Table 3). Stall (18) reported up to 50% disease incidence in resistant tomato cultivars, and attributed this high incidence to the effect of inoculum concn and environmental conditions. In this study, penetrance was affected by the interaction of host genotype and any external factor tested. Thus, under all experimental conditions, penetrance was lower in heterozygous lines than in the respective homozygous ones, as found also by Retig et al. (16). The cultivar Homestead 24 displayed a relatively high degree of penetrance compared with Roma VF, and a comparison between the two respective heterozygous F_1 lines showed the same trend. The very low disease incidence in Homestead 24 was also reported in other studies (5, 9, 16). The difference in degree of penetrance between Homestead 24 and Roma VF (both of the *II* genotype), as well as between other homozygous cultivars (5), may be attributed to a

TABLE 6. Population level of *Fusarium oxysporum* f. sp. *lycopersici* in tissues of inoculated, but apparently healthy, tomato seedlings of two resistant genotypes, as estimated by the dilution and the segmentation techniques

Cultivar and Genotype	Part of Plant[b]	A. Dilution technique[a], 1,000 propagules/g dry tissue — Experiment no. 1	2	3
Homestead 24 × Marmande (*Ii*)	Root	3.92	7.26	0
	Stem 1	0.71	0	0
	Stem 2	0	0	0
Homestead 24 (*II*)	Root	2.96	6.05	17.29
	Stem 1	0	0	0
	Stem 2	0	0	0

		B. Segment technique[c], % Fusarium infected segments — Experiment no. 1	2	3	4
Homestead 24 × Marmande (*Ii*)	Root	30	42	4	13
	Stem 1	10	10	4	8
	Stem 2	0	0	0	0
Homestead 24 (*II*)	Root	30	18	16	12
	Stem 1	0	2	1	8
	Stem 2	0	0	0	0

[a]Tissues were macerated in a Waring Blendor, diluted, and spread over solidified agar medium. *Fusarium* colonies obtained were counted, and population density (no. propagules/g dry tissue) was calculated.

[b]Plants were cut into three sections: roots, 0-1 cm aboveground (stem 1), and 4-5 cm aboveground (stem 2).

[c]Plant segments (2-mm long) were plated out on agar medium and % of segments yielding *Fusarium* was determined.

difference in accompanying modifying genes (4) which are strongly affected by environmental changes, as has been demonstrated in many cases of field resistance (20, 21).

Each tested factor had a different effect upon the resistant and susceptible lines. Various amounts of inoculum were required to cause a certain level of disease incidence in each line (Table 1). It was previously reported that final disease incidence of F_1 seedlings inoculated 10 days postemergence, was similar to that of younger plants but that disease progress was slower with the former (16). In the present experiments, the penetrance of resistance increased substantially with the increase in seedling age.

Soil temp had a pronounced effect on penetrance. At a low temp (17 C), disease incidence of the susceptible Marmande decreased; whereas, that of the resistant lines increased compared with the 27 C temp (Table 3). Environmental conditions, such as temp, may affect disease through the pathogen, the efficacy of the host's resistance mechanism, or the activities of the prevailing microflora. The strikingly different response of susceptible and resistant cultivars to changes in temp should be attributed to the different response of the host, since all other factors are equal. The defense mechanisms in susceptible and resistant cultivars are controlled by different genetic systems, thus their response to rather low temp are not necessarily similar. It is therefore suggested that with resistant cultivars, a decrease in temp from 27 C to 17 C impairs the host defense mechanism; e.g., sealing-off of vascular infections (2) or suppression of enzyme production by the fungus (15), more than it affects the growth and aggressiveness of the pathogen. The opposite seems to occur in the susceptible cultivar. It is well-known that temp affects resistance of plants to various pathogens; e.g., *Verticillium albo-atrum* in mint (3), stem rust in oat (14), and *Rhizoctonia solani* in cotton (8). At low temp, disease incidence caused by *Gibberella saubinettii* was high in corn, but low in wheat (7). In tomatoes, Strong (19) found less Fusarium wilt at low temp with both a susceptible and a partially resistant cultivar ('Marglobe'). However, the latter cultivar does not possess monogenic type of resistance (21), as do the cultivars used in this study. Certain amino acids increased Fusarium disease development in Homestead 24 (10). Because increased root exudation of amino acids at low temp was observed (8), the possible relations between these phenomena in resistant tomato cultivars deserves further study.

Although a certain percentage of heterozygous resistant plants were classified as diseased, they displayed a lower disease severity than diseased plants of the susceptible cultivar Marmande. This was manifested in criteria such as disease symptoms, disease progress, xylem discoloration, population level, fungal distribution in various plant parts, and water conductibility. The fungus under study, even though restricted in its pathogenicity to tomatoes, invades tissues of many plants, including resistant tomato cultivars: in such cases, however, its colonization is restricted to the lower parts of the plants (2, 11, 13, 15 and Table 6). Thus, the significantly reduced population level of the pathogen in the upper part of diseased plants of resistant genotypes, as compared with the susceptible one, is one of the manifestations of their relatively lower disease-severity.

Although F_1 plants carry a dominant allele for resistance, the incidence of disease among them was higher and more affected by environmental conditions than among the homozygous resistant parents. These expressions of incomplete penetrance should be taken into consideration when producing F_1 hybrids adapted to widely varying environmental conditions.

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