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LINKAGE IN *SPINACIA OLERACEA* L. OF TWO RACE-SPECIFIC GENES FOR RESISTANCE TO DOWNY MILDEW *PERONOSPORA FARINOSA* F. SP. *SPINACIAE* BYFORD

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SUMMARY

The genetics of resistance to races 1 and 2 of downy mildew *Peronospora farinosa* f. sp. *spinaciae* in the spinach variety 'Nores' was investigated in crosses and backcrosses with the susceptible variety 'Eerste Oogst'. Resistance appears to be governed by two closely linked genes in coupling phase with a recombination percentage of 4.6.

INTRODUCTION

Spinach (*Spinacia oleracea* L.) varieties which are resistant to race 2 of the downy mildew *Peronospora farinosa* f. sp. *spinaciae* BYFORD are also resistant to race 1 of the fungus. This may be a result of a) one pleiotropic resistance gene, or b) two very closely linked resistance genes (in coupling phase). This paper indicates which of the above possibilities applies.

MATERIALS AND METHODS

Crosses were made between plants of spinach cv. 'Eerste Oogst' (E) as female parents and plants of cv. 'Nores' (N) as male parents. 'Eerste Oogst' is susceptible to race 1 and race 2 of downy mildew and Nores is resistant to both races. Resistance inherites dominantly (see e.g. EENINK, 1974). F1 (E × N) plants were backcrossed with plants of 'Eerste Oogst' resulting in B1 (E × (E × N) populations.

Both parents, F1 and B1 populations were tested for resistance to race 1 and race 2 of the downy mildew. Each plant was tested for resistance to race 1 and race 2 separately. Tests for resistance to race 1 were made with leaf discs (EENINK, 1973) and the young plants from which these discs were obtained, were tested for resistance to race 2 (RODENBURG & VAN RAALTEN, 1959). 'Eerste Oogst' and 'Nores' were tested because sometimes in varietal spinach populations plants occur with deviating genotypes for resistance. The F1 populations were tested for the homozygosity of the genotype for resistance of the 'Nores' male parent plants.

RESULTS AND DISCUSSION

If resistance in 'Nores' against race 1 and race 2 should be governed by one gene or by two genes with close linkage in coupling phase, then genotypic frequencies can be expected to occur in the different populations as indicated in Table 1.

The results of the tests for resistance to race 1 and race 2 of the B1 plants and of the parents are shown in Table 2. From this table it appears that all plants of the control varieties were either resistant ('Nores') or susceptible ('Eerste Oogst') to both races. This indicates that no escapes occurred and also that reliable test results were obtained for the B1 plants because these were tested at the same time and under the same conditions. Table 2 shows that there were B1 plants which appeared to be resistant to race 1 and susceptible to race 2 and vice versa. It is not very likely that these reaction patterns originate from escapes in testing for resistance, because a few B1 plants with the reaction pattern + – (see Table 2) were isolated and subjected for paired crosses. The resulting populations were tested for resistance to race 2 and appeared to segregate for this resistance. Apparently the B1 plants used for the crosses had the genotypes *aaBb* for resistance (see also Table 1) where the gene *B* gives resistance to race 2. So the distribution of the B1 plants over the different reaction patterns, as is shown in Table 2 in connection with the theoretical genotype frequencies of Table 1, suggests that one gene (*A*) governs resistance to race 1 and one gene (*B*) governs resistance to race 2. These genes are apparently linked in coupling phase. From the distribution over the four reaction patterns shown in Table 2, the recombination percentage appears to be 4.6. This suggests that linkage is very close.

Table 1. Hypothetical resistance genotypes for parental, F1, and B1 populations. p = recombination frequency.

Population	One resistance gene (*A–a*)	Two resistance genes (*A–a, B–b*)
Eerste Oogst (E)	*aa*	*aabb*
Nores (N)	*AA*	*AABB*
F1 (ExN)	*Aa*	*AaBb*
B1 (Ex(ExN))	$^1/_2$ *Aa*, $^1/_2$ *aa*	$^1/_2$ (1–p) *AaBb*, $^1/_2$ p *Aabb*, $^1/_2$ p*aaBb*, $^1/_2$ (1–p) *aabb*

Table 2. Distribution of plants of parental and backcross populations over four possible reaction patterns after inoculation with races 1 and 2 of downy mildew. + = susceptible; – = resistant.

Reaction pattern		Type of population		
Race 1	Race 2	Nores (N)	Eerste Oogst (E)	B1 (E(ExN))
+	+	0	30	128
+	–	0	0	10
–	+	0	0	3
–	–	30	0	139
Total number of plants		30	30	280

CONCLUSIONS

Resistance to races 1 and 2 of downy mildew appears to be governed by two genes which are closely linked in coupling phase. In plants with heterozygous allelic pairs crossing over may occur between these genes leading to loss of one of the two resistances. Consequently it is of great importance in downy mildew resistance breeding to test certain populations not only with race 2 as is done usually, but also with race 1.

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REFERENCES

EENINK, A. H., 1973. Een methode om een spinazieplant te toetsen op zowel resistentie tegen *Peronospora spinaciae* (Wolf) als op tolerantie voor komkommervirus 1 (Mozaiek). Zaadbelangen 12: 238–239.

EENINK, A. H., 1974. Linkage in *Spinacia oleracea* L. between the locus for resistance to *Peronospora spinaciae* Laub. and the locus for tolerance for cucumber virus 1. Euphytica 23: 485–487.

RODENBURG, C. M. & W. J. VAN RAALTEN, 1959. Het kunstmatig besmetten van spinazierassen met wolfsporen. Zaadbelangen 13: 186.